VEGETATION CLASSIFICATION AND SURVEY

International Association for Vegetation Science (IAVS)

Vegetation Classification and Survey 6: 191–208
doi: 10.3897/VCS.154417

RESEARCH PAPER

CLASSIFICATION OF EUROPEAN FORESTS

Ravine forests in Colchis (Georgia) – Azonal forests in a Tertiary relict flora hotspot

Pavel Novák[1], Veronika Kalníková[2], Vojtěch Taraška[3], Nino Memiadze[4], Davit Kharazishvili[4]

1 *Department of Botany and Zoology, Faculty of Science, Masaryk University, Brno, Czech Republic*
2 *Beskydy Protected Landscape Area Administration, Rožnov pod Radhoštěm, Czech Republic*
3 *Moravian museum, Department of Botany, Brno, Czech Republic*
4 *Batumi Botanical Garden, Batumi, Georgia*

Corresponding author: Pavel Novák (pavenow@seznam.cz)

Academic editor: Idoia Biurrun ♦ **Linguistic editor:** Meena Sritharan
Received 2 April 2025 ♦ **Accepted** 16 August 2025 ♦ **Published** 29 September 2025

Abstract

Azonal communities of ravine forests are often confined to pristine sites, and represent habitats with species-rich biota. Despite their significance for conservation biology, little attention has been paid to this vegetation in the Caucasus, one of the global biodiversity hotspots. **Aims:** (a) to describe the variability, ecology, and distribution patterns of ravine forests at lower elevations of Colchis in Georgia; (b) to examine the syntaxonomic position of Colchic and Caucasian ravine forests; and (c) to outline the relationships between the identified vegetation types and environmental as well as biogeographic factors. **Study area:** Georgia, Türkiye. **Methods:** Two classification analyses (*beta*-flexible clustering) were performed; the first on vegetation plots of ravine forests (n = 45) from Georgian Colchis, the second on an extended dataset (n = 134) that included additional plots of Caucasian ravine forests and the alliance *Alnion barbatae*. NMDS was applied to visualize patterns of similarity among the communities. **Results:** Three associations of Colchic ravine forests were distinguished, mainly reflecting the climate and bedrock: *Polysticho woronowii-Ulmetum glabrae* (wet climate, volcanics), *Pterido creticae-Tilietum begoniifoliae* (wet climate, limestones), and *Polysticho aculeati-Tilietum begoniifoliae* (drier climate, limestones). The classification of the extended dataset resulted in two main clusters, Colchic alluvial forests (*Populetalia albae*) and scree and ravine forests (*Aceretalia pseudoplatani*). A further partitioning distinguished between Caucasian and Colchic ravine forests. The latter represent a newly established alliance *Pterido creticae-Tilion begoniifoliae*, characterised by a wealth of Colchic endemic and relict species. These forests are of particular importance for safeguarding the Colchic forest biota. **Conclusions:** The variability of the Colchic ravine forests primarily reflects site-specific and climatic conditions, which allow their classification into three distinct associations. These stands constitute a novel alliance which complements the so-far known vegetation diversity of the prominent Colchic forests, a hotspot of Tertiary relict flora in the Northern Hemisphere.

Taxonomic reference: Euro+Med PlantBase (https://europlusmed.org/) [accessed 10 Oct 2024].

Syntaxonomic reference: Higher syntaxa follow Mucina et al. (2016), exceptions and associations are accompanied by their author citations at the first mention.

Abbreviations: DCA = Detrended Correspondence Analysis; GIVD = Global Index of Vegetation-Plot Databases; NMDS = Non-Metric Multidimensional Scaling; TWINSPAN = Two Way Indicator Species Analysis.

Keywords

Aceretalia pseudoplatani, azonal forest community, Caucasus, Colchis, deciduous forest, phytosociology, syntaxonomy, *Tilia*, vegetation

PENSOFT

Copyright *Pavel Novák et al.* This is an open access article distributed under the terms of the Creative Commons Attribution License (CC-BY 4.0), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

Introduction

Ravine forests represent azonal plant communities confined to sites with skeletal and colluvial soils on steep, shady and often rocky slopes and their bases. They are shaped by relatively frequent natural disturbances, including landslides, debris flows and solifluction. Their soils are often nutrient- and humus-rich, well-aerated, and developed on a variety of bedrock. They preferentially colonize landforms like gullies, ravines, or hillsides (Clot 1990; Košir et al. 2008; Campos et al. 2011; Millar 2014; Chytrý et al. 2020). Numerous deciduous noble hardwood tree species prevail in their canopy in Western Eurasia, particularly of the genera *Acer*, *Fraxinus*, *Tilia* and *Ulmus*. These species are relatively shade-tolerant and cope with unstable substrates by extensive root systems with a considerable regenerative capability. Their understory is very diverse in terms of species composition, reflecting the parent rock, disturbance regime, and climatic and biogeographic factors (Clot 1990; Košir et al. 2008; Campos et al. 2011; Mucina et al. 2016; Leuschner and Ellenberg 2017; Chytrý et al. 2020; Zukal et al. 2020).

Ravine forests are identified as communities preserving rich forest biota even in otherwise highly deforested areas as they often escaped intensive forestry practices (Stefańska-Krzaczek et al. 2016; Baran et al. 2018; Leuschner and Ellenberg 2017). Besides ecosystem services generally provided by forests and other wooded areas (Aznar-Sánchez et al. 2018), ravine forests are vital for soil erosion control, slope stabilization and natural disaster risk reduction (Leuschner and Ellenberg 2017). They are threatened by numerous factors such as illegal logging, invasions of alien species, tree pathogen outbreaks, rock mining, construction activities and extreme climatic events (Thalmann et al. 2015; Janssen et al. 2016; Chytrý et al. 2019). Accordingly, the revised Annex I to Resolution No. 4 of the Bern Convention lists them among endangered habitats (Council of Europe 2018). Ravine forests constitute a distinctive component of the vegetation mosaic of the mountain ranges in the nemoral zone of Western Eurasia (Košir et al. 2008; Campos et al. 2011; Mucina et al. 2016; Leuschner and Ellenberg 2017). The EuroVegChecklist, a revised hierarchical list of European Braun-Blanquet syntaxa down to the category of alliance, recognizes these forests as the phytosociological order *Aceretalia pseudoplatani* (Mucina et al. 2016), which corresponds to the EUNIS habitat type T1F Ravine forest (Chytrý et al. 2020).

The Caucasus, ranked among the global biodiversity hotspots (Mittermeier et al. 2004), also harbors these communities (Akhalkatsi and Tarkhnishvili 2012; Nakhutsrishvili 2013; Fayvush and Aleksanyan 2016; Novák et al. 2019, 2020). A crucial area for the Caucasian forest diversity is the Colchic refugium (hereafter "Colchis"), located in the southwest of the hotspot. Colchis primarily consists of coastal lowlands along the Black Sea and adjacent slopes of the Caucasus and Pontic Range. It shelters one of the most prominent Tertiary relict floras in the Northern Hemisphere (Rübel 1914; Denk et al. 2001; Milne and Abbott 2002; Milne 2006; Nakhutsrishvili 2013; Gegechkori 2020). The region was relatively less affected by the Quaternary climatic oscillations associated with cooling and aridization, which allowed entire communities of broadleaved deciduous forests to persist here through the Last Glacial Maximum (Tarasov et al. 2000; Connor et al. 2007). This unusual climatic stability was probably critical for the survival of a wealth of Tertiary plant lineages, including laurophyllous shrubs and lianas (Milne and Abbott 2002; Milne 2006). The current Colchic climate is typically warm-temperate and year-round humid. Characteristic high precipitation originates in wet air masses that rise from the Black Sea and are blown by prevailing westerly winds over the mountainous mainland. Additionally, the barrier of the Greater Caucasus prevents Colchis from expansions of dry and cold air from the northeast, which has a crucial mitigating effect in mostly frost-free winters (Kikvidze and Ohshawa 2001; Ghafarian et al. 2012; Bondyrev et al. 2015). Colchis has been permanently heavily populated at least since the first millennium BP, which resulted in vast deforestation and other significant environmental changes, especially at low elevations (Connor et al. 2007; Bokeria 2010; Bondyrev et al. 2015). The relatively recent introduction of many crops of foreign, often Eastern Asian, origin and trade intensification, coupled with the favourable climate, resulted in the invasion of numerous alien plants across the Colchic landscape (Kikodze et al. 2010; Gegechkori 2020).

Ravine forests are regionally considered among phytosociologically understudied forest types due to their azonal character, poor accessibility and limited extent (Košir et al. 2008; Campos et al. 2011; Zukal et al. 2020). For instance, *Tilia begoniifolia*, presumably the most common dominant tree of Georgian ravine forests, forms only 1.5% of the total forested area of the country (MEPA 2023). Just a small number of vegetation plots of ravine forests have been available in Georgia to date (Novák et al. 2019, 2020; Nakhutsrishvili et al. 2024). Moreover, because of their predominantly poly-dominant tree layer, ravine forests were poorly reproduced by the dominant-oriented vegetation classification formerly applied in Georgia (e.g. Sinskaia 1933; Gulisashvili et al. 1975; Dolukhanov 2010). Georgian Natura 2000 habitat typology recognized them as the unit "9180GE *Tilio-Acerion* forests of slopes, screes and ravines" (Akhalkatsi and Tarkhnishvili 2012).

Georgian ravine forests have been phytosociologically studied in the central and eastern Greater Caucasus, where the alliance *Pachyphragmo macrophyllae-Tilion begoniifoliae* Zukal in Novák et al. 2021 was described, with two associations, *Valeriano tiliifoliae-Ulmetum glabrae* Zukal in Novák et al. 2021 and *Hedero pastuchovii-Aceretum velutini* Zukal in Novák et al. 2021 (Novák et al. 2020, 2021b). An additional association was reported from the southwesternmost Colchic part of the country. It was described from the volcanic massif Achara-Imereti Range as *Polysticho woronowii-Ulmetum glabrae* Zukal in

Novák et al. 2019 (Novák et al. 2019). Otherwise, ravine forests of the majority of Georgian Colchis have not been phytosociologically studied so far, although their presence was briefly mentioned in the literature (e.g. Kolakovskii 1961; Dolukhanov 1980) and the strongly dissected relief of some forested areas, often built up by limestones (Adamia 2010; Tielidze 2019), anticipates much larger diversity of this vegetation. Novák et al. (2019) assigned *Polysticho-Ulmetum* to the alliance *Alnion barbatae* Quézel et al. ex Quézel et al. 1992. However, there were also striking floristic differences between *Alnion barbatae* and *Polysticho-Ulmetum*, which were difficult to interpret based on the data available at the time of publication. Moreover, the alliance's original description (Quézel et al. 1980, 1992) was somewhat ambiguous. Nevertheless, the prevailing viewpoint (e.g. Korkmaz et al. 2008; Ermakov et al. 2021) regarded it as Colchic alluvial forests. Therefore, in this study we also focus on clarifying the syntaxonomic position of the alliance *Alnion barbatae* and the association *Polysticho woronowii-Ulmetum glabrae* in light of new data on Colchic ravine forests.

Specifically, we addressed the following goals: 1) To outline the variability, ecology and distribution patterns of ravine forests at lower elevations of Colchis in Georgia. 2) To examine the syntaxonomic position of the Colchic and Caucasian ravine forests and that of the alliance *Alnion barbatae*. 3) To outline relationships between the recognized vegetation types and environmental and biogeographic factors.

Study area

We conducted our field survey in the Colchic region of Georgia, representing the eastern section of the Euxinian Province, Circumboreal Region of the Holarctic (Takhtajan 1986). This region is limited in Georgia by the Black Sea in the west and the slopes of the Lesser and the Greater Caucasus, connected by the Likhi Range, making its south, north and east boundaries, respectively (Nakhutsrishvili et al. 2011). The natural forest vegetation of the Caucasian slopes exhibits a characteristic vertical zonation with mixed *Castanea sativa* and *Carpinus betulus* forests in the lower belt (up to ~1000 m), *Fagus orientalis* in the middle (~1000–1500 m) and relict coniferous trees (*Abies nordmanniana*, *Picea orientalis*) forming the upper forest belt (up to ~2000 m). Subalpine elfin forests with *Acer trautvetteri* and *Betula* spp. constitute the uppermost forest belt (around 2000 m) (Kolakovskii 1961; Gagnidze and Kemularia-Natadze 1985; Zazanashvili 1999). However, local environmental conditions (Sokhadze and Sokhadze 1964) and human activities (Bokeria 2010; Akhalkatsi 2015; Gegechkori 2020) have markedly altered this general zonation. We focused on the diversity of ravine forests in the first vegetation belt. Our sampling covered a variety of bedrock types. The southern part (Adjara and Guria regions) encompasses slopes of the Lesser Caucasus (Adjara-Imereti Range) and Guria Range, primarily formed by Cenozoic volcanic rock. On the contrary, the northern part (Samegrelo and Imereti regions) shows a typical karst landscape on Mesozoic limestones of the Greater Caucasus forelands (Adamia 2010). The study area belongs to the maritime subtropical humid climate region (Mumladze and Lomidze 2012). The average annual precipitation varies considerably (1000–4000 mm) with temperatures ranging from 10–14 °C. Winter temperatures may occasionally drop below freezing, mainly in rugged terrain distant from the sea (Tielidze 2019). The relation between the geographic names of the Caucasus and Colchis is ambiguous. In this study, we distinguish between "Colchic" and "Caucasian" ravine forests as biogeographically distinct, with the latter encompassing ravine forests in the Caucasus outside the Colchic area (Nakhutsrishvili et al. 2011).

Methods

Data sampling and datasets

We led the field sampling of 38 original vegetation plots (relevés; Suppl. material 1) in Georgian Colchic during the vegetation seasons between 2017 and 2023, applying the Braun-Blanquet approach (Dengler et al. 2008). On steep slopes and their bases, we recorded plots that were dominated by noble hardwood trees (sensu Clot 1990; Angiolini et al. 2012) typical of local ravine forests (*Acer cappadocicum*, *Fraxinus excelsior*, *Tilia begoniifolia*, *Ulmus glabra*; Kolakovskii 1961; Nakhutsrishvili 2013; Novák et al. 2019), while trees of zonal forests (*Carpinus betulus*, *Castanea sativa*, *Fagus orientalis*; Dolukhanov 2010; Nakhutsrishvili 2013) were absent or reached only low covers and did not prevail. This combination of conditions is the key characteristic of European ravine forests (Chytrý et al. 2020). We estimated the percentage cover of vascular plant vegetation layers (tree, shrub, herb) in square plots 10 m × 10 m. Only in a few cases, when the square-shaped plot could not be placed, we used a rectangular plot of the same area. We assessed species covers in each layer using the extended Braun-Blanquet cover-abundance scale (Dengler et al. 2008). As juveniles, we identified individuals of woody plants not exceeding ~50 cm in height, except for lianas in the herb layer, which were considered herbs. We acquired plot coordinates (WGS 84) using a GPS receiver and then determined the following variables: slope inclination, aspect, elevation, and percentage covers of the moss layer and rocks. We took four subsamples of 15 cm of the topsoil in each plot and mixed them into one sample. Then, we measured the pH of the dried sample (fraction ≤ 2 mm) in a suspension with deionized water (2:5) using the instrument Greisinger GMH 3530. We digitized the plots in Turboveg 2.1 (Hennekens and Schaminée 2001) and stored them in the Transcaucasian Vegetation Database (Novák et al. 2023a; GIVD ID AS-00-005).

We analysed two datasets to address the goals of the study. To assess the variability of the Colchic ravine forests, we compiled the dataset "Colchic Ravine Forests" (n = 45). It combined seven published plots of the association *Polysticho woronowii-Ulmetum glabrae* (Novák et al. 2019) dominated by noble hardwood trees and 38 original plots collected during the aforementioned field sampling (Suppl. material 1). The second dataset, "Regional Forests" (n = 134), served to examine differences between Colchic and Caucasian ravine forests and to clarify the position of the alliance *Alnion barbatae* (class *Alno glutinosae-Populetea albae,* order *Populetalia albae;* Kavgacı et al. 2023) into which the association *Polysticho woronowii-Ulmetum glabrae* was originally assigned.

Caucasian ravine forests of the alliance *Pachyphragmo macrophyllae-Tilion begoniifoliae* were represented by both of the associations described to date: *Valeriano tiliifoliae-Ulmetum glabrae* and *Hedero pastuchovii-Aceretum velutini* (Novák et al. 2020, 2021b). The associations of the alliance *Alnion barbatae* included *Thelypterido-Alnetum barbatae* Quézel et al. ex Quézel et al. 1992 (Quézel et al. 1980) and *Diospyro loti-Alnetum barbatae* Korkmaz et al. 2008 (Korkmaz et al. 2008) from the Black Sea coast of northern Anatolia, *Sedo stoloniferi-Alnetum barbatae* Novák et al. 2023 from relatively warm and humid river valleys on the transition between the Greater Caucasus and Colchis in Georgia (Novák et al. 2023b), as well as two communities published under the provisional association names *Carici remotae-Pterocaryetum pterocarpae* and *Truello thurnbergii-Alnetum barbatae* from the Abkhazia region in northwestern Georgia (Ermakov et al. 2021). Details on the plots from the literature are provided in Suppl. material 2. In both datasets, we removed bryophyte records that were determined only in a small fraction of plots and vascular plant records identified only at the genus level. Afterwards, we aggregated several hard-to-distinguish and taxonomically complicated taxa (Suppl. material 3). In the Regional Forests dataset, we merged same-name species across the vegetation strata, applying the formula by Fischer (2015) because most of the plots from the literature lacked vegetation layer data. We calculated the number of all vascular plant species, alien species (Kikodze et al. 2010) and Georgian endemic species (Gagnidze 2005) for each plot in the Colchic Ravine Forests dataset. Given the prominent ecological role of evergreen shrubs and lianas in Colchis (Dolukhanov 1980; Nakhutsrishvili et al. 2011; Nakhutsrishvili 2013), we assessed the cover of evergreen woody species using the same strategy as above (Fischer 2015).

To investigate the vegetation-climate relationship, we extracted the following plot climatic variables from the BIOCLIM+ dataset in the Chelsa database (Brun et al. 2022a, 2022b, period 1981–2010): annual mean temperature (BIO1), temperature seasonality (BIO4), annual precipitation (BIO12) and precipitation seasonality (BIO15). We applied this procedure only for plots of the Colchic Ravine Forests dataset due to high uncertainty in the geographic localization of plots from the literature. We processed spatial data using QGIS 3.8 (QGIS Development Team 2018).

Data analysis

For numerical analysis purposes, Braun-Blanquet cover-abundance values were transformed to percentage cover values using the default transformation available in the Juice 7.1 software (Tichý 2002; Tichý et al. 2011). We conducted a series of classification analyses to examine the structure and internal variability of the datasets using commonly applied agglomerative and divisive methods like *beta*-flexible clustering (Lance and Williams 1967), Ward's method (Ward 1963) and modified TWINSPAN (Roleček et al. 2009). Percentage cover values were square-root transformed prior to the two former analyses (Tichý et al. 2020), while pseudospecies cut levels (0%, 5%, 25%) were used in the latter (Hill et al. 1975). All classification analyses were computed in Juice 7.1 (Tichý 2002). We applied OptimClass1 (Tichý et al. 2010) to search for the partitioning option that yielded the highest number of diagnostic species. *Beta*-flexible clustering based on Bray-Curtis distance was identified as the optimal approach. Diagnostic species were identified according to the phi coefficient expressing species-to-cluster fidelity (Sokal and Rohlf 1995) with virtually equalized clusters (Tichý and Chytrý 2006). Fisher's exact test was calculated to exclude species with statistically insignificant concentrations ($P > 0.05$) in a cluster from diagnostic species lists. Highly diagnostic (phi ≥ 0.5), diagnostic (phi ≥ 0.25), constant (frequency ≥ 25%) and dominant species (cover ≥ 25%) were determined for each cluster. Further analyses were computed in R 4.2.2 (R Core Team 2022). We employed the Kruskal-Wallis test to assess inter-cluster differences in the vegetation and environmental variables within the Colchic Ravine Forests dataset. When we found a significant difference ($P \leq 0.05$), we calculated Dunn's test (R package *FSA*, Ogle et al. 2023) to identify heterogeneous pairs of clusters ($P \leq 0.05$). To visualize patterns of similarities among the vegetation types of the Regional Forests dataset, we computed NMDS with Bray-Curtis dissimilarity. The analysis was performed with square-root transformed percentage cover values using the R package *vegan* (Oksanen et al. 2022). In the syntaxonomic sections, we adhered to the rules of the latest edition of the International Code of Phytosociological Nomenclature (Theurillat et al. 2021).

Results

Colchic ravine forests – diversity, distribution, ecology

We analysed relevés in the Colchic Ravine Forests dataset sampled on various bedrock across the lower

areas of Georgian Colchis (45–1,060 m a.s.l.) that were dominated mainly by *Acer cappadocicum*, *Tilia begoniifolia* and *Ulmus glabra*. The average slope inclination reached 54° and a rock cover of 35%, indicating relatively harsh site conditions for the development of forests. The forests were found to have relatively well-developed tree (average cover 76%), shrub (33%), herb (56%) and moss layers (29%). The dataset contained 186 species in total, 84 of which reached a frequency above 10%. Average plot species richness was 31. These forests were revealed to harbor a wealth of Colchic endemic and subendemic taxa. Their most frequent representatives encompassed *Hedera colchica* (37 records), *Trachystemon orientalis* (30), *Ruscus colchicus* (29), *Vinca major* subsp. *hirsuta* (20), *Ilex colchica* (18), *Polystichum woronowii* (15), *Prunus laurocerasus* (14), *Staphylea colchica* (13), *Hypericum xylosteifolium* (12) and *Rhododendron ponticum* (10). Georgian endemics were represented mainly by *Symphytum grandiflorum* (15). Other common understory species were *Asplenium scolopendrium* (43), *Pteris cretica* (29), *Dioscorea communis* (28), *Asplenium trichomanes* (26) and *Smilax excelsa* (26). Alien species were rather uncommon in this dataset, except for two of them (*Oplismenus hirtellus* subsp. *undulatifolius* and *Potentilla indica*), which occurred in more than a quarter of plots. Others were much less common, including escaped cultivated trees (e.g. *Juglans ailantifolia*, *Robinia pseudoacacia*) and weeds (e.g. *Erigeron annuus*, *Phytolacca americana*). The pattern of distribution of Colchic laurophyllous species is outlined in the community descriptions. They were represented mainly by shrub individuals, while their rare seedlings indicated prevailing vegetative propagation by natural layering of branches.

Within the dataset, we recognized three clusters produced by the *beta*-flexible clustering (*beta* = -0.5). Below, we provide an overview, including alphabetically ordered lists of diagnostic and dominant species. For species recorded in more vegetation layers, we provide the relevant layer in brackets. They are accompanied by community geographic distribution (Figure 1), box-plots for environmental variables (Figure 2), pictures of typical stands (Figure 3), a table of tested means and standard deviations of vegetation and environmental variables (Table 1) and a synoptic table of diagnostic species (Table 2). Their diagnostic, constant and dominant species are listed in the Suppl. material 4.

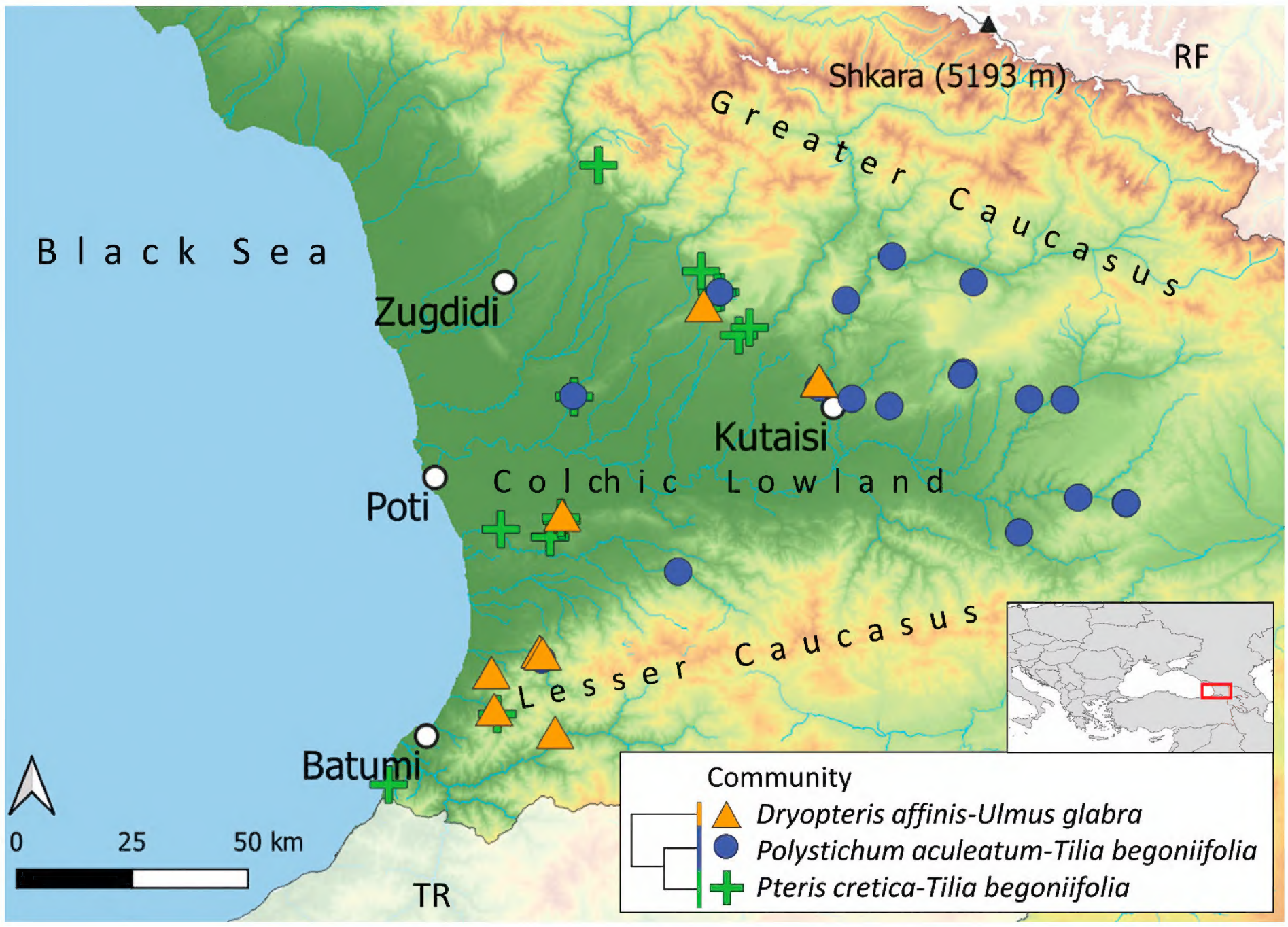

Figure 1. Geographic distribution of Colchic ravine forest plots (n = 45), showing their community assignments. The classification dendrogram of the unsupervised analysis is included in the legend, adjacent to the community names.

Table 1. Means and standard deviations of vegetation, site and climatic variables of the recognized communities, and Kruskal-Wallis *H* and *p*-value resulting from the Kruskal-Wallis test. The variables with statistically significant differences (*p*-value ≤ 0.05) are in bold. Different letters in mean values indicate significant between-pair differences based on the Dunn's test (*P* ≤ 0.05).

	Dryopteris-Ulmus **n = 10**	***Polystichum-Tilia*** **n = 19**	***Pteris-Tilia*** **n = 16**	***H***	***p*-value**
Vegetation variables					
Number of species	29.0 ± 4.4	30.6 ± 8.8	32.8 ± 8.7	1.44	0.487
Number of alien species	**1.2 ± 1.6 (ab)**	**0.4 ± 0.6 (a)**	**1.8 ± 1.0 (b)**	14.47	0.001
Number of Georgian endemics	**0.6 ± 0.7 (a)**	**1.1 ± 1.5 (a)**	**2 ± 1.7 (b)**	6.74	0.034
Cover of tree layer (%)	70 ± 14	78 ± 12	77 ± 12	2.94	0.230
Cover of shrub layer (%)	40 ± 19	32 ± 20	30 ± 19	1.95	0.377
Cover of evergreen shrubs (%)	19 ± 17	12 ± 19	9 ± 15	3.42	0.181
Cover of herb layer (%)	59 ± 17	55 ± 15	55 ± 14	0.79	0.674
Cover of moss layer (%)	**24 ± 24 (a)**	**16 ± 19 (a)**	**46 ± 19 (b)**	14.30	0.001
Site variables					
Elevation (m)	**268 ± 92 (a)**	**516 ± 279 (b)**	**245 ± 123 (a)**	11.44	0.003
Soil pH	6.4 ± 0.9	7.0 ± 0.6	7.0 ± 0.6	2.83	0.243
Slope (°)	**52 ± 16.6 (ab)**	**44.9 ± 19.5 (ac)**	**66.3 ± 13.4 (b)**	10.98	0.004
Cover of rocks (%)	**32 ± 34 (ab)**	**21 ± 28 (a)**	**54 ± 28 (b)**	8.40	0.015
Climatic variables					
Annual temperature (°C)	**13.2 ± 0.6 (a)**	**11.3 ± 1.7 (b)**	**13.1 ± 0.9 (a)**	15.82	0.001
Annual precipitation (mm)	**2,756 ± 558 (a)**	**1,808 ± 505 (b)**	**2,461 ± 383 (a)**	19.71	0.001
Temperature seasonality	**686 ± 37 (a)**	**758 ± 39 (b)**	**698 ± 40 (a)**	19.15	0.001
Precipitation seasonality	**25.0 ± 8.1 (a)**	**15.3 ± 5.2 (b)**	**20.0 ± 8.2 (ab)**	7.16	0.028

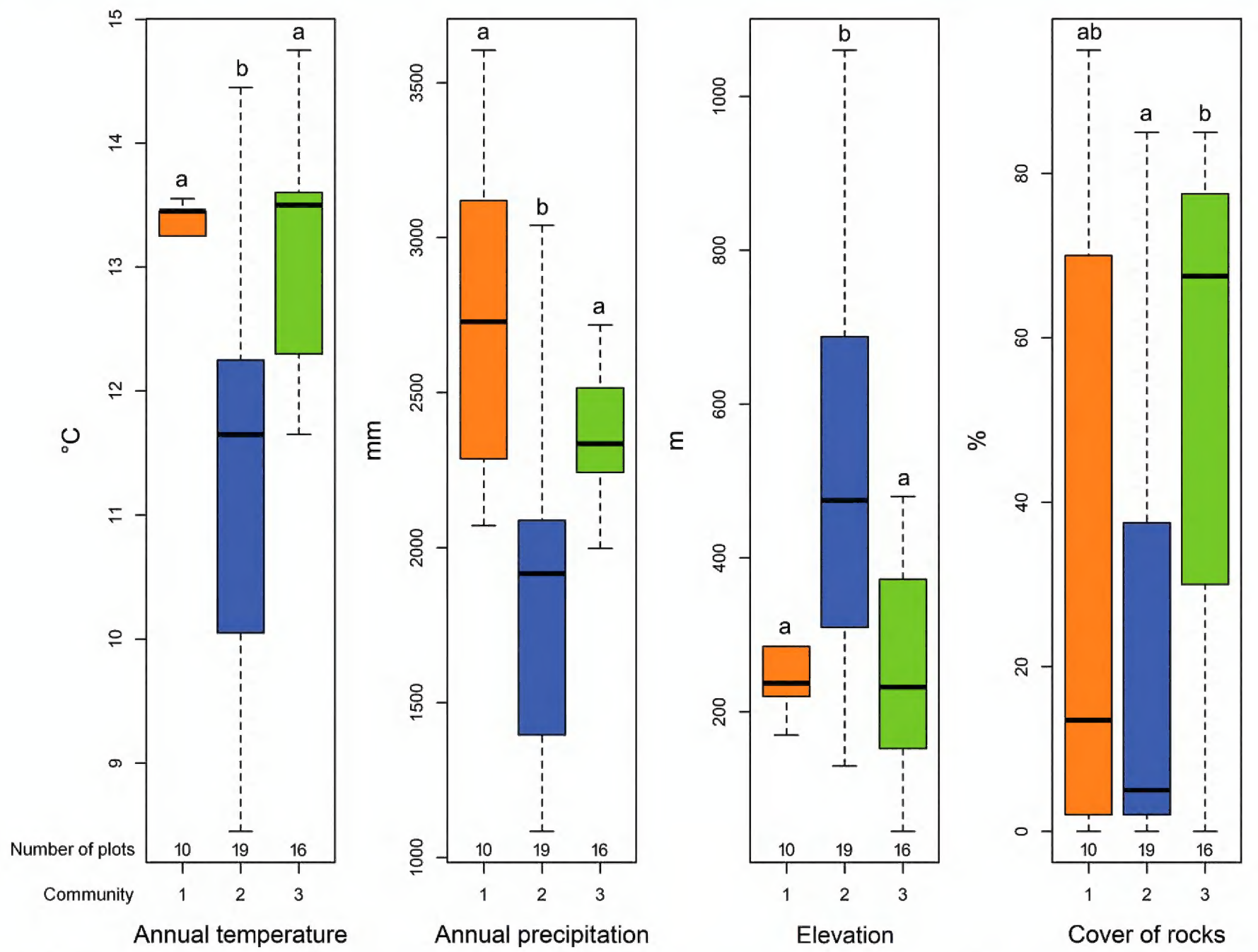

Figure 2. Boxplots of selected environmental variables for the communities of the Colchic Ravine Forests dataset. Horizontal lines within the boxes represent medians, boxes indicate 25–75% interquartile range and whiskers show the range of values without outliers. The letters above the boxes identify homogeneous groups (Dunn's test, *P* > 0.05). Communities (associations): 1 – *Dryopteris affinis-Ulmus glabra* (*Polysticho-Ulmetum*), 2 – *Polystichum aculeatum-Tilia begoniifolia* (*Polysticho-Tilietum*), 3 – *Pteris cretica-Tilia begoniifolia* (*Pterido-Tilietum*).

1 – *Dryopteris affinis-Ulmus glabra* community (10 plots)

Diagnostic species: *Alnus glutinosa* subsp. *barbata* (tree), *Aruncus dioicus*, *Blechnum spicant*, *Cardamine wiedemanniana*, *Castanea sativa* (tree), *Dryopteris affinis* s.l., *Hypericum xylosteifolium*, *Ilex colchica* (tree), *Ulmus glabra* (tree).

Dominant species: *Acer cappadocicum* (tree), *Alnus glutinosa* subsp. *barbata* (tree), *Carpinus betulus* (tree), *Fagus orientalis* (tree), *Hedera colchica* (herb), *Hedera helix* (herb), *Hypericum xylosteifolium* (shrub), *Prunus laurocerasus* (shrub), *Rhododendron ponticum* (shrub), *Rubus* subgen. *Rubus*, *Ruscus colchicus*, *Sambucus nigra* (shrub), *Staphylea pinnata* (shrub), *Ulmus glabra* (tree), *Ulmus laevis* (tree).

Ecology and distribution: This community mainly unifies ravine forests on the windward slopes of the volcanic Adjara-Imereti Range. They thrived in a relatively warm and wet climate (mean annual temperature 13.2 °C and annual precipitation 2,756 mm), lacking summer dry periods. The bedrock was rather acidic; furthermore, soil cations were leached by the high rainfall. The cover of rocks was intermediate among the recognized communities.

Structure and composition: *Acer cappadocicum* and *Ulmus glabra* mostly dominated the canopy, with a characteristic admixture of *Alnus glutinosa* subsp. *barbata* and *Castanea sativa*. The understory exhibited an extraordinarily high cover of evergreen species. The relatively dense shrub layer combined laurophyllous (*Ilex colchica*, *Rhododendron ponticum*) and deciduous elements (e.g. *Sambucus nigra*, *Staphylea pinnata*). The field layer was distinctive by the occurrence of oceanic ferns (*Blechnum spicant*, *Dryopteris affinis* s.l.) and ravine forest specialists, including *Aruncus dioicus*, a tall forb well-adapted to solifluction. The broad-leaved clonal taxa *Hedera colchica* and *Rubus* subgen. *Rubus* mostly dominated this layer. The average plot species richness reached 29 species. The share of alien species in the community was intermediate (1.2 species per plot) and *Oplismenus hirtellus* subsp. *undulatifolius* was the most common representative. The moss layer was generally well-developed (average cover 24%), preferentially colonizing rock outcrops. We adopted the association name *Polysticho woronowii-Ulmetum glabrae* for this community as most of its relevés included in the analysis (5 of 7, including the holotypus), were classified within, along with several original relevés.

2 – *Polystichum aculeatum-Tilia begoniifolia* community (19 plots)

Diagnostic species: *Cardamine bulbifera*, *Carpinus betulus* (juvenile), *Euonymus latifolius* (juvenile), *Helleborus orientalis*, *Lactuca muralis*, *Lathyrus vernus*, *Polygonatum multiflorum*, *Polystichum aculeatum*, *Tilia begoniifolia* (tree).

Dominant species: *Acer campestre* (tree), *Acer cappadocicum* (tree), *Aruncus dioicus*, *Buxus sempervirens* (shrub), *Carpinus betulus* (tree), *Carpinus orientalis* (tree), *Castanea sativa* (tree), *Corylus avellana* (shrub), *Fraxinus excelsior* (tree), *Hedera colchica* (herb), *Hedera helix* (herb), *Oplismenus hirtellus* subsp. *undulatifolius*, *Rhododendron ponticum* (shrub), *Rubus* subgen. *Rubus*, *Staphylea colchica* (tree), *Tilia begoniifolia* (tree), *Ulmus glabra* (tree).

Ecology and distribution: The community occupied less rocky limestone slopes (average cover of rocks 21%) in cooler and drier climate (mean annual temperature 11.3 °C and annual precipitation 1,808 mm) compared to the other communities. It was associated with slightly leeward areas of hills and plateaus, distant from the Black Sea coast and thus less affected by maritime air masses. It was documented in limestone ravines and gorges in NE Colchis, mainly in the Imereti Region. The soil reaction of the stands was primarily neutral (average pH 7.0).

Structure and composition: *Tilia begoniifolia* usually dominated the canopy, with an admixture of the zonal trees *Carpinus betulus* and *Castanea sativa*. The shrub layer mixed laurophyllous (mainly *Ilex colchica*) and deciduous species (e.g. *Corylus avellana*, *Euonymus latifolius*), including young tree individuals. *Buxus sempervirens* used to form a thick understory in places before its recent dieback. The herb layer contained common species of the Colchic ravine forests, but some of them were found considerably rare in this cluster (e.g. *Polystichum woronowii*, *Pteris cretica*), presumably due to less humid climate. Many nemoral herbs were diagnostic (e.g. *Cardamine bulbifera*, *Lathyrus vernus*). *Asplenium trichomanes*, *Polypodium vulgare* s.l. and *Polystichum aculeatum* represented species of rock crevices. The share of alien species was the lowest among the communities, averaging 0.4 species per plot. Moreover, they were only present in a third of the plots. The average species richness reached 30.6 species per plot. The relatively low cover of rocks was associated with a mostly low cover of mosses.

3 – *Pteris cretica-Tilia begoniifolia* community (16 plots)

Diagnostic species: *Adiantum capillus-veneris*, *Carex digitata*, *Cicerbita petiolata*, *Lamium galeobdolon*, *Oplismenus hirtellus* subsp. *undulatifolius*, *Pachyphragma macrophyllum*, *Philadelphus coronarius*, *Polystichum setiferum*, *P. woronowii*, *Potentilla indica*, *Prunus laurocerasus* (shrub), *Pteris cretica*, *Salvia glutinosa*, *Saxifraga cymbalaria*, *Klasea quinquefolia*, *Tilia begoniifolia* (tree), *Urtica dioica*.

Dominant species: *Castanea sativa* (tree), *Fraxinus excelsior* (tree), *Hedera colchica* (herb), *Hedera helix* (herb), *Lamium galeobdolon*, *Prunus laurocerasus* (shrub), *Tilia begoniifolia* (tree).

Ecology and distribution: The community was recorded in low limestone hills. It was characteristic of the Caucasian forehills in the Samegrelo Region and the Guria Range, closer to the coastline than the previous community. The annual precipitation and temperature were higher, averaging 2,461 mm and 13.1 °C, respectively. The community colonized neutral soils associated with limestones. Its stands were the rockiest of the recognized communities, related to topographically diverse karst landscapes.

Figure 3. Colchic ravine forests. **A.** Stand of the association *Polysticho-Ulmetum* on volcanic bedrock, Adjara Region; **B.** Forest of the association *Polysticho-Tilietum* in a shallow limestone valley, Samegrelo Region; **C.** Stand of the association *Pterido-Tilietum* in a deep limestone ravine, Samegrelo Region; **D.** Stand of the association *Pterido-Tilietum* at the bottom of a limestone ravine, Samegrelo Region; **E.** Karst river valleys in the Imereti region are rich in ravine forests; **F.** Dieback of *Buxus sempervirens* in ravine forests in humid limestone valleys, Samegrelo Region. Photos: P. Novák.

Structure and composition: *Tilia begoniifolia* prevailed in the canopy, whereas zonal trees were scarce or missing. The shrub layer combined deciduous species, including the remarkable Colchic endemic *Staphylea colchica*, and laurophyllous elements, particularly *Prunus laurocerasus*. The herb layer was diverse and mostly lacked distinctive dominants. Stoloniferous and rhizomatous species that cope with moving substrates (e.g. *Hedera colchica*, *Lamium galeobdolon*) played an essential role in bioindication. Ferns were frequent, especially *Asplenium scolopendrium* and *Pteris cretica*, accompanied by broadly distributed forest mesophytes (e.g. *Dioscorea communis*, *Salvia glutinosa*). However, the species spectrum of forest generalists (e.g. *Brachypodium sylvaticum*, *Carex digitata*) was revealed poorer than in the previous communities. Indicators of humid rock outcrops (e.g. *Adiantum capillus-veneris*,

Table 2. Shortened synoptic table of the Colchic ravine forest communities. Given values represent frequency values (%). Highly diagnostic (phi ≥ 0.5; grey-shaded, in bold) and diagnostic species (phi ≥ 0.25; grey-shaded) of the communities are listed, sorted according to decreasing phi. The ten most frequent non-diagnostic species are given below them, sorted by decreasing frequency. Species names are accompanied by their vegetation layers (tree, shrub, herb, juveniles – tree and shrub individuals in the herb layer). Communities (associations): 1 – *Dryopteris affinis-Ulmus glabra* (*Polysticho-Ulmetum*), 2 – *Polystichum aculeatum-Tilia begoniifolia* (*Polysticho-Tilietum*), 3 – *Pteris cretica-Tilia begoniifolia* (*Pterido-Tilietum*). See Suppl. material 5 for the full version.

Community		**1**	**2**	**3**
Number of plots		**10**	**19**	**16**
Species	**Layer**			
***Dryopteris affinis-Ulmus glabra* community**				
Dryopteris affinis s.l.	herb	70	21	19
Ulmus glabra	tree	60	11	19
Castanea sativa	tree	80	37	25
Aruncus dioicus	herb	50	16	6
Alnus glutinosa subsp. *barbata*	tree	50	5	19
Hypericum xylosteifolium	shrub	30	.	6
Cardamine wiedmanniana	herb	20	.	.
Blechnum spicant	herb	20	.	.
Ilex colchica	tree	20	.	.
***Polystichum aculeatum-Tilia begoniifolia* community**				
Lathyrus vernus	herb	.	26	.
Euonymus latifolius	juvenile	.	26	.
Cardamine bulbifera	herb	.	21	.
Polygonatum multiflorum	herb	.	21	.
Helleborus orientalis	herb	.	21	.
Lactuca muralis	herb	.	26	6
Polystichum aculeatum	herb	40	58	6
Carpinus betulus	juvenile	.	32	13
***Pteris cretica-Tilia begoniifolia* community**				
Potentilla indica	herb	10	.	**75**
Polystichum setiferum	herb	.	.	**38**
Urtica dioica	herb	.	16	50
Polystichum woronowii	herb	40	.	69
Pteris cretica	herb	90	21	100
Oplismenus hirtellus subsp. *undulatifolius*	herb	40	26	81
Pachyphragma macrophyllum	herb	.	11	38
Carex digitata	herb	10	32	63
Prunus laurocerasus	shrub	20	5	50
Cicerbita petiolata	herb	10	5	38
Saxifraga cymbalaria	herb	20	11	50
Adiantum capillus-veneris	herb	.	.	19
Klasea quinquefolia	herb	.	5	25
Philadelphus coronarius	shrub	10	11	38
Salvia glutinosa	herb	30	42	69
Lamium galeobdolon	herb	50	16	63
Species diagnostic for two clusters				
Tilia begoniifolia	tree	.	**100**	94
Other frequent species				
Asplenium scolopendrium	herb	90	95	100
Hedera colchica	herb	70	74	75
Trachystemon orientalis	herb	80	53	75
Ruscus colchicus	herb	60	63	69
Dioscorea communis	herb	20	74	75
Corylus avellana	shrub	50	63	63
Asplenium trichomanes	herb	70	58	50
Carpinus betulus	tree	50	63	25
Vinca major subsp. *hirsuta*	herb	30	42	56
Acer cappadocicum	juvenile	60	58	19

Saxifraga cymbalaria) locally enriched the understory, while *Polystichum woronowii* and *Ruscus colchicus* represented the most frequent Colchic endemics. The community showed the highest share of alien species, averaging 1.8 per plot. The most common ones included *Oplismenus hirtellus* subsp. *undulatifolius* and *Potentilla indica*, both herbaceous species invading the community through intensive vegetative propagation and zoochory. The plot species richness

was the highest among the recognized communities (32.8 species on average). Due to higher air humidity and significant stand rockiness, the moss layer reached comparably high cover values. Moreover, epiphytic bryophytes often formed thick layers on tree trunks and branches.

Colchic ravine forests in the regional context

To examine the relationships of the Colchic ravine forests with their Caucasian counterparts (alliance *Pachyphragmo macrophyllae-Tilion begoniifoliae*) and the alliance *Alnion barbatae*, we classified (*beta*-flexible clustering, *beta* = -0.3) the Regional Forests dataset. The analysis produced two main clusters (Figure 4), one for the ravine forests (phytosociological class *Carpino-Fagetea*) and one for the alluvial forests (phytosociological class *Alno glutinosae-Populetea albae*). Communities of the Colchic ravine forests were found to be more closely related to the Caucasian ravine forests than to the Colchic alliance *Alnion barbatae* whose plots formed the second main cluster. It indicated that fundamental similarities in the site conditions outweighed climatic and biogeographic factors in this division. The principal partitioning of the ravine forest cluster distinguished Colchic and Caucasian stands. The resulting three clusters of the Regional Forests dataset were interpreted at the alliance level. The interpreted classification dendrogram and the NMDS diagram are provided in Figure 4, and the synoptic table listing their diagnostic species in the Suppl. material 6. The alluvial forest main cluster showed high inner heterogeneity, presumably because its clusters were located on a broad geographic and climatic gradient of the southern Black Sea coast. Colchic ravine forests were well-separated from the associations of the alliance *Alnion barbatae*, although some species were shared.

The floristic characteristics of the *Alnion barbatae* alliance based on the results of the classification analysis are: (a) predominance of the relict deciduous trees *Alnus glutinosa* subsp. *barbata* or *Pterocarya fraxinifolia* in the canopy; (b) occurrence of shade-tolerant nutrient- and moisture-demanding generalists (*Geum urbanum*, *Glechoma hederacea*, *Ranunculus repens*, *Rubus caesius*) coupled with wetland species (e.g. *Carex remota*, *Lycopus europaeus*); (c) rarity or absence of specialized trees of Colchic and Caucasian ravine forests (*Tilia begoniifolia* and *Ulmus glabra* in particular); and (d) rarity or absence of species of rock crevices and non-waterlogged stony soils, especially members of the genus *Polystichum* and some other ferns (e.g. *Pteris cretica*) and dicots (e.g. *Arabis nordmanniana*). The same applies to nemoral species avoiding moist or waterlogged soils (*Carex digitata*, *Drymochloa drymeja*). Moreover, the increased soil moisture and occasional floods act as environmental filters, excluding a large portion of local native tree species from the communities of the alluvial forests. A group of shared species between the ravine and alluvial forests includes mainly nutrient-demanding forest specialists and some other shade-tolerant herbs (e.g. *Athyrium filix-femina*, *Lamium galeobdolon*, *Salvia glutinosa*, *Urtica dioica*). In terms of environmental conditions reported in the literature, soils of stands were primarily characterized as hydromorphic, developed in various topographic conditions, including river floodplains and waterlogged depressions.

In contrast, the Colchic ravine forests showed a relatively species-rich canopy dominated by noble hardwoods, especially *Acer cappadocicum*, *Tilia begoniifolia* and *Ulmus glabra*, whereas *Alnus glutinosa* subsp. *barbata*, *Carpinus betulus* and *Castanea sativa* could be admixed. The understory contained numerous evergreen species, including shrubs (e.g. *Ilex colchica*, *Prunus laurocerasus*), lianas (e.g. *Hedera colchica*, *Smilax colchica*) and species of the herb layer (e.g. *Ruscus colchicus*, *Vinca major* subsp. *hirsuta*). Further, Colchic endemics and subendemics were characteristic of the forest floor (e.g. *Trachystemon orientalis*, *Polystichum woronowii*). Common ferns of rock crevices (*Asplenium trichomanes*, *Polypodium vulgare* s.l.) and regionally widespread forest mesophytes (e.g. *Carex digitata*, *Potentilla micrantha*, *Salvia glutinosa*) accompanied them. Typical species of European ravine forests exhibited relatively high frequency (e.g. *Aruncus dioicus*, *Asplenium scolopendrium*, *Polystichum aculeatum*).

The classification of the ravine forest main cluster separated two Caucasian associations described in the literature and three Colchic communities reported above (Figure 4). Floristic differences between the Caucasian and Colchic ravine forests were significant, although they shared numerous species. A group of laurophyllous species and Colchic endemics positively delimited the Colchic stands from the Caucasian. Additionally, Caucasian stands were found richer in broadly distributed nemoral (e.g. *Galium odoratum*, *Polygonatum multiflorum*, *Primula veris* subsp. *macrocalyx*) and Eastern Caucasian-Hyrcanian species (e.g. *Acer velutinum*, *Hedera pastuchovii*) while in Colchic submediterranean and oceanic species (e.g. *Dioscorea communis*, *Ficus carica*, *Pteris cretica*) were more abundant.

The Caucasian ravine forest associations constitute the alliance *Pachyphragmo macrophyllae-Tilion begoniifoliae*. By contrast, there is no available name for the alliance assembling the three Colchic ravine forest associations recognized in this study. Therefore, we describe here the new alliance *Pterido creticae-Tilion begoniifoliae* all. nov. It includes the association *Polysticho woronowii-Ulmetum glabrae*, as well as two more associations, which are also newly described here as *Polysticho aculeati-Tilietum begoniifoliae* ass. nov. and *Pterido creticae-Tilietum begoniifoliae* ass. nov. Their formal descriptions are provided in the syntaxonomic outline at the end of the study. The broadly accepted phytosociological typology of forests in Europe and adjacent areas (Mucina et al. 2016) applies mainly ecological criteria reflected in dominant tree genera and/or overall species composition at the level of classes and orders. By contrast, alliances have mostly biogeographic meaning, mirroring distribution patterns of narrow-range forest species and thus presumably reflecting Quaternary

forest refugia (Willner et al. 2017; Novák et al. 2023c). The newly described alliance *Pterido-Tilion* (order *Aceretalia pseudoplatani*) complements the diversity of the upper syntaxa recognized in the Euxinian Province (Çoban and Willner 2019; Kavgacı et al. 2023), including zonal oak-hornbeam forests (alliance *Trachystemono orientalis-Carpinion betuli* Çoban & Willner 2019), *Fagus orientalis* forests (e.g. suballiance *Piceo orientalis-Fagenion orientalis* Kavgacı et al. 2023) and coniferous forests (e.g. *Abietion equi-trojani* Kavgacı et al. 2023). The new alliance contains three formally described associations based on our results: *Polysticho woronowii-Ulmetum glabrae* (*Dryopteris affinis-Ulmus glabra* community), *Polysticho aculeati-Tilietum begoniifoliae* (*Polystichum aculeatum-Tilia begoniifolia*) and *Pterido creticae-Tilietum begoniifoliae* (*Pteris cretica-Tilia begoniifolia*).

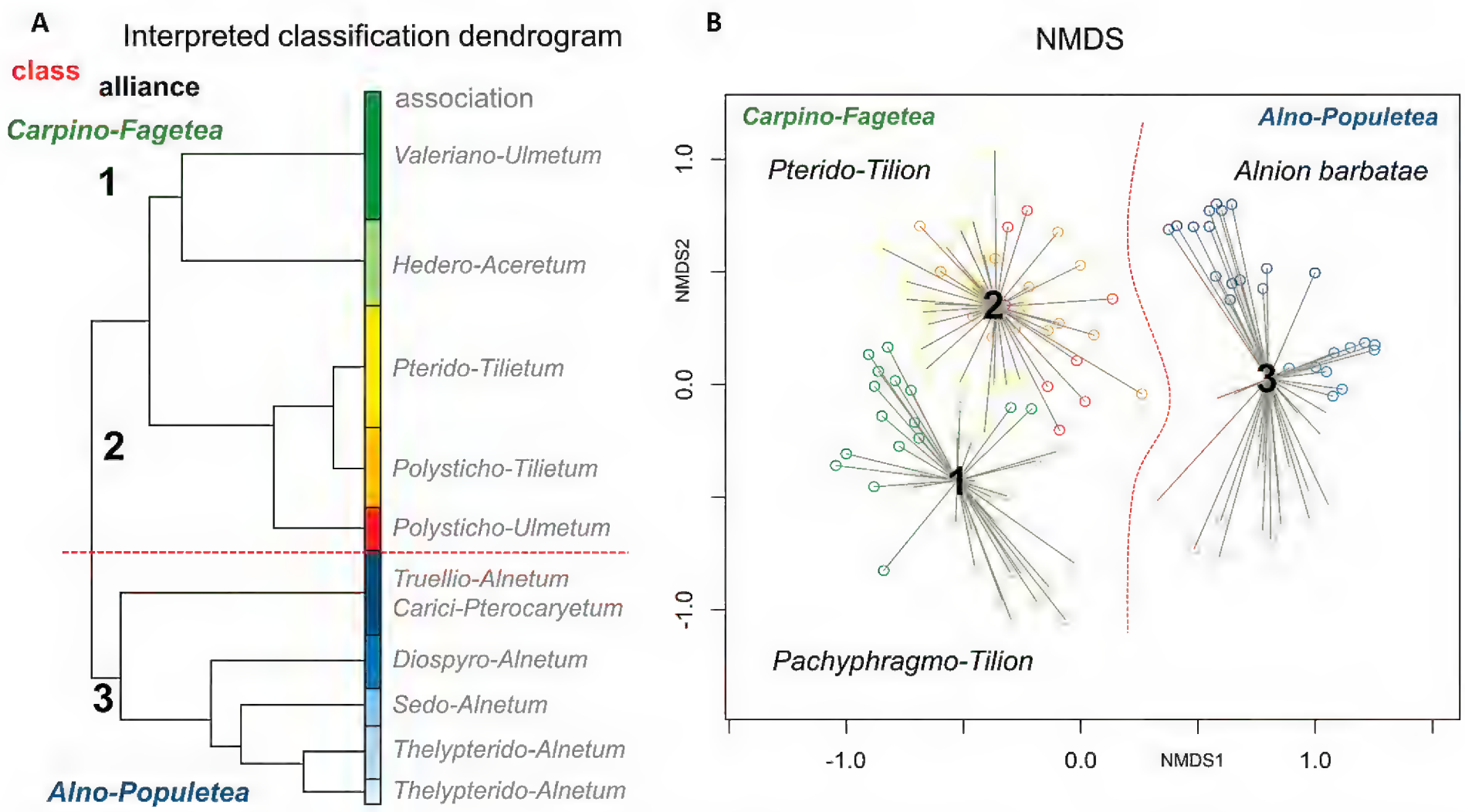

Figure 4. A. Interpreted classification dendrogram (*beta*-flexible clustering, *beta* = -0.3); **B.** NMDS diagram (stress 0.202) of the Regional Forests dataset with the analysed plots. Plots are distinguished according to the colour (cluster) and grouped into alliances (spider plots) with numbered alliance centroids. The dashed red line divides two classes.

Discussion

Patterns in species richness and species composition of the Colchic ravine forests

The species richness of the Colchic ravine forests was not significantly different among the recognized communities. Averaging 29–33 species per 100 m^2, it was found to be intermediate among European deciduous forests (cf. Večeřa et al. 2019). Species composition of the Colchic ravine forests reflected complex gradients of local (bedrock type, cover of rock) and broad-scale environmental variables (climate). Similar complex patterns in species assemblages of ravine forests (order *Aceretalia pseudoplatani*) were reported from central and southern Europe, and were reflected in a substantial number of described associations (Willner and Grabherr 2007; Campos et al. 2011; Valachovič et al. 2021). Our results indicated a high concentration of Colchic endemic and relict species in the local ravine forests. This observation is consistent with previous observations (e.g. Maleev 1938; Kolakovskii 1961; Bebiia 2022). *Ilex colchica* and *Prunus laurocerasus* were the two most frequent representatives of laurophyllous shrub flora, probably the most distinctive vegetation attributes of Colchic forests (Dolukhanov 1980; Kikvidze and Ohshawa 2001; Nakhutsrishvili et al. 2011). Both species are relatively drought-enduring, capable of growing on shallow calcareous soils and grow optimally in areas with annual precipitation exceeding 1,100–1,400 mm (Zazanashvili 1999). However, the former copes relatively well with lower temperatures and decreased air humidity and, therefore, thrives better in mountain forests, while the latter finds its optimum in forested ravines eroded in limestones in mountain foothills (Dolukhanov 1980). The third most common Colchic shrub, *Rhododendron ponticum*, generally avoids calcareous soils and areas with annual rainfall below 1,300 mm (Dolukhanov 1980; Zazanashvili 1999). *Buxus sempervirens* (syn. *B. colchica*), another evergreen shrub, was recorded in several plots. However, its former distribution in Colchic ravine forests is difficult to estimate because it has been rapidly declining over the last fifteen years as a result of the co-invasion of the fungal pathogen *Cylindrocladium buxicola* (Gorgiladze et al. 2011) and the moth *Cydalima perspectalis* (Matsiakh et al.

2018). The distribution pattern of laurophyllous species across the described clusters is consistent with previously reported ecological requirements (Dolukhanov 1980; Zazanashvili 1999).

Along with xero-mesophilous and xerophilous forests with *Carpinus orientalis* (alliance *Smilaco excelsae-Carpinion orientalis* Novák et al. 2024), ravine forests are an important component of the diversity of azonal forests of Georgian Colchis. The former preferentially inhabit sunny and rocky slopes on limestone bedrock (Novák et al. 2021a, 2024), while ravine forests are confined to shaded sites typically occurring in their vicinity.

Based on the classification analysis, we found Caucasian ravine forests described from central and eastern Georgia (*Pachyphragmo macrophyllae-Tilion begoniifoliae*) to be substantially different from the Colchic ravine forests (*Pterido creticae-Tilion begoniifoliae*). The latter contains the association *Polysticho aculeati-Tilietum begoniifoliae*, which, although it has the lowest proportion of characteristic species of Colchic forests, still shelters laurophyllous (e.g. *Hedera colchica*) and deciduous (e.g. *Staphylea colchica*) woody species and herbs (e.g. *Trachystemon orientalis*) symptomatic for Colchis (Denk et al. 2001; Nakhutsrishvili 2013). It, therefore, represents a transition towards the Caucasian ravine forests (*Pachyphragmo-Tilion*) but still belongs to the alliance *Pterido-Tilion*. Conversely, a similar numerical comparison with ravine forests from the Anatolian part of the Euxinian Province was not possible due to a lack of data. Regional phytosociological syntheses (Quézel et al. 1980; Çoban and Willner 2019; Kavgacı et al. 2023) reported no specific syntaxa dominated by ravine forest noble hardwoods. Moreover, these tree species appeared only in a very limited number of their plots, where they mostly reached low cover. Two *Tilia platyphyllos*-dominated plots, which Quézel et al. (1980) classified under the variability of beech forests in the alliance *Buxo-Staphylion* Quézel et al. (1980) 1992, made an exception. Additionally, Anşin (1979) presented two plots with prevalence of *Ulmus glabra* in his study on spruce stands, however, without syntaxonomic assignment. The regionally small number of available plots of the given vegetation type could be due to its reported restricted occurrence (Güngöroğlu 2018), along with its position outside the main focus of vegetation scientists due to its azonal nature and tendency to occur in inaccessible sites, similar to some other regions (cf. Košir et al. 2008; Baran et al. 2018; Zukal et al. 2020).

Position of the alliance *Alnion barbatae*

The alliance *Alnion barbatae* was first published (invalidly) by Quézel et al. (1980) and validated by the same authors (Quézel et al. 1992). However, due to the relative heterogeneity of the original phytosociological relevés, its interpretation remained ambiguous (Novák et al. 2019; Kavgacı et al. 2023). Quézel et al. (1980) provided the following diagnostic species (originally ordered): *Alnus barbata* (= *A. glutinosa* subsp. *barbata*), *Thelypteris limbosperma*, *Frangula alnus*, *Prenanthes cacaliaefolia* (= *Cicerbita petiolata*), *Circaea lutetiana*, *Rhychochoris elephas* (= *Rhynchocorys elephas*), *Aruncus sylvester* (= *Aruncus dioicus*), *Hypericum androsaemum*, *Gentiana asclepiadea*, *Cardamine raphanifolia*, *C. lazica* (= *C. wiedemanniana*), *Heracleum crenatifolium*, *Lamium album*, *Petasites hybridus* and *Chrysosplenium dubium*. According to this list, the only subordinate association published by the authors seemed to be rather hygrophilous, including forest spring specialists (e.g. *Chrysosplenium dubium*, *Cardamine* spp.). Their plots originated from hydromorphic silicate soils covering mild slopes along a large elevation gradient (10–1,550 m a.s.l.). Diagnostic species of the European ravine forests (Chytrý et al. 2020) were missing, except for *Aruncus dioicus*, which commonly penetrates alluvial forests in mountains and their foothills (Tüxen 1957; Neuhäuslová-Novotná 1974; Quézel et al. 1980). The list of original diagnostic species of *Alnion barbatae* and the position of the plots accompanying the original alliance description in the context of *Alnus glutinosa* subsp. *barbata* forests described in the eastern part of Colchis (Figure 4) clearly support its interpretation as alluvial forests, which follows the assumption of some authors (Ermakov et al. 2021; Kavgacı et al. 2023; Novák et al. 2023b). The previous perspective that included the association *Polysticho woronowii-Ulmetum glabrae* into the alliance *Alnion barbatae* (Novák et al. 2019) was based on the scarce phytosociological data from the SW part of Georgian Colchis available at that time. However, we conclude that the association *Polysticho woronowii-Ulmetum glabrae* should be placed outside the alliance *Alnion barbatae*, within the variability of ravine forests. The ecology of *A. glutinosa* subsp. *barbata* itself in the hyperhumid areas of the Black Sea region deserves more attention. The tree is not limited to sites affected by groundwater but might climb up steep, shaded slopes, as observed from the Adjara region in Georgia (e.g. Golitsyn 1935; Dolukhanov 1980). These studies considered such alder stands as early successional stages after extensive timber extraction from forests with different dominants and interpreted the spread of alder as being supported by the region's highly humid climate. This stage was believed to survive only a limited period if the establishment of late-successional and more shade-tolerant trees was not blocked or considerably slowed by disturbances or dense and tall understory. This is particularly relevant given that *A. glutinosa* seedlings are light-demanding and the species hardly rejuvenates in closed-canopy forests (Leuschner and Ellenberg 2017). Hence, it appears that alder might be naturally admixed in Colchic ravine forests as a result of disturbances associated with climatic peculiarities. Nevertheless, the data on the successional trends of Colchic forests based on long-term monitoring have not yet been established.

Other related communities

In areas bordering the Euxinian and Caucasian Provinces (Takhtajan 1986), specialized ravine forest communities have been studied mainly in the Balkans (e.g. Košir et al. 2008). The newly described alliance *Pterido-Tilion* has the geographically closest described alliance of the order *Aceretalia pseudoplatani* in the Balkans, where the alliance *Ostryo carpinifoliae-Tilion platyphylli* was designated for low-elevation ravine forests. A shared group of broadly distributed submediterranean-oceanic forest herbs (e.g. *Asplenium scolopendrium*, *Dioscorea communis*, *Polystichum setiferum*) or their Euxinian/Colchic geographic vicariants (e.g. *Daphne laureola* – *D. pontica*, *Primula acaulis* subsp. *acaulis* – *P. acaulis* subsp. *rubra*) highlights their biogeographic connections. Ravine forests in Crimea are presumably relatively rare and confined to its topographically diverse southern shore (Didukh 1996, 2016). The local type is dominated by the endemic tree *Acer hyrcanum* subsp. *stevenii* thriving on stony limestone slopes in the mountain belt. Constant and character species of this community include *Acer hyrcanum* subsp. *stevenii*, *Anthriscus sylvestris*, *Arum elongatum*, *Cardamine quinquefolia*, *Carpinus betulus*, *Fraxinus excelsior*, *Galanthus plicatus*, *Galium odoratum*, *Mercurialis perennis* and *Primula acaulis*. Their syntaxonomic classification to higher syntaxa remains unclear (cf. Didukh 1996, 2016). In any case, Caucasian and Colchic elements are missing.

The second prominent area of the Tertiary relict flora in the Caucasus hotspot, the Hyrcanian refugium (Nakhutsrishvili et al. 2015; Gholizadeh et al. 2020), also harbors forests with a characteristic presence of noble hardwoods (e.g. *Acer cappadocicum*, *Tilia rubra*). The alliance *Ilici spinigerae-Taxion baccatae* Karami-Kordalivand et al. 2021 described from northern Iran unifies stands with a mixture of the coniferous *Taxus baccata* and noble hardwoods. Members of the Hyrcanian floral element (e.g. *Acer velutinum*, *Ruscus hyrcanicus*) are widespread (Karami-Kordalivand et al. 2021). However, they also contain a group of common species with Colchic and Caucasian forests (e.g. *Acer cappadocicum*, *Prunus laurocerasus*) and diagnostic species of ravine forests of Western Eurasia (e.g. *Asplenium scolopendrium*, *Mercurialis perennis*, *Polystichum aculeatum*). The classification of this alliance to higher syntaxa was not provided due to its problematic class assignment (Karami-Kordalivand et al. 2021). Finally, Ermakov et al. (2023) presented *Fagus orientalis* forests (order *Rhododendro pontici–Fagetalia orientalis* Passarge 1981) with some species of ravine forests from climatically humid areas of Abkhazia (northwestern Georgia) under the name *Thlaspio macrophylli–Fagion orientalis* Ermakov et al. 2023. These forests were recorded on milder slopes than the Colchic ravine forests and were mostly dominated by zonal tree species. Moreover, diagnostic species of the described Colchic ravine forests (e.g. *Arabis nordmanniana*, *Polystichum woronowii*, *Pteris cretica*) were rare or absent. Beech forests with an admixture of ravine forest specialists have been reported from central, southern and southeastern Europe (Biondi et al. 2002; Chytrý 2013; Coldea 2015; Valachovič et al. 2021). They have been assigned under the beech forest syntaxa and often regarded as a transition towards ravine forests, favouring steeper slopes and shallower soil.

Conservation remarks

The reported communities of Colchic ravine forests shelter a wealth of endemic taxa limited to Colchic or Colchic-Caucasian areas. Considering formerly published data (e.g. Dolukhanov 1980; Zazanashvili 1999; Novák et al. 2019, 2020), some species appear to reach their optimum in Colchic ravine forests. They include herbs (e.g. *Polystichum woronowii*, *Symphytum grandiflorum*), shrubs, both evergreen (e.g. *Prunus laurocerasus*) and deciduous (*Staphylea colchica*, see also Vetters and Tribsch 2008), and even trees (*Tilia begoniifolia*). Previous studies have emphasized the exceptional role of the ravine forests in supporting Colchic plant diversity (e.g. Maleev 1938; Kolakovskii 1961; Bebiia 2022) underlined by a high concentration of Colchic relict and endemic species. Therefore, their adequate protection is of the utmost importance to conserve the genetic heritage of the Colchic forests. Although they are partly situated within the boundaries of protected areas with a special management regime (e.g. national parks – Machakhela, Mtirala; protected landscapes – Machakhela; reserves – Sataplia; Emerald candidate sites – Machakhela, Mtirala, Samegrelo) (EU4Environment 2024), the majority of stands remain outside. Currently, forest stands on slopes steeper than 35° enjoy the legal status of Protection forests as defined in the Forest Code of Georgia (Parliament of Georgia 2020). This category also includes forests in eroded areas or on slopes prone to landslides and forests within the 100 m buffer zone around cliffs, screes, karst landforms and landslides. The objective of the management of a protection forest is to preserve and enhance the forest protective function, whereas commercial timber harvesting and subsoil extraction are prohibited. Nevertheless, ensuring compliance with legal protective conditions to avoid further forest degradation and deforestation remains challenging throughout the Caucasus (Akhalkatsi 2015).

Syntaxonomic outline

Class: *Carpino-Fagetea sylvaticae* Jakucs ex Passarge 1968
Order: *Aceretalia pseudoplatani* Moor 1976
Alliance: *Pterido creticae-Tilion begoniifoliae* all. nov. hoc loco
Association: *Polysticho woronowii-Ulmetum glabrae* Zukal in Novák et al. 2019
Association: *Polysticho aculeati-Tilietum begoniifoliae* ass. nov. hoc loco
Association: *Pterido creticae-Tilietum begoniifoliae* ass. nov. hoc loco

***Pterido creticae-Tilion begoniifoliae* all. nov. hoc loco**

Holotypus: *Pterido creticae -Tilietum begoniifoliae* ass. nov. hoc loco

Diagnostic species: *Acer cappadocicum*, *Arabis nordmanniana*, *Asplenium scolopendrium*, *A. trichomanes*, *Buxus sempervirens*, *Carex pendula* s.l., *Cicerbita petiolata*, *Clinopodium umbrosum*, *Dryopteris affinis* s.l., *Ficus carica*, *Hedera colchica*, *Ilex colchica*, *Polystichum woronowii*, *Prunus laurocerasus*, *Pteris cretica*, *Ruscus colchicus*, *Saxifraga cymbalaria*, *Smilax excelsa*, *Staphylea colchica*, *Tilia begoniifolia*, *Trachystemon orientalis*, *Ulmus glabra*, *Vinca major* subsp. *hirsuta*.

Absolute character taxon (sensu Willner 2020): *Polystichum woronowii*

Ecology: These forests colonize ravines and shaded steep slopes, often rocky or those with scree accumulations. Sites are generally prone to landslides and solifluction. The soils are skeletal and colluvial, mostly nutrient- and humus-rich, well-aerated and developed on a variety of bedrock.

***Pterido creticae-Tilietum begoniifoliae* ass. nov. hoc loco**

Pteris cretica-Tilia begoniifolia community in this study

Holotypus: Relevé 31 in the Suppl. material 1. Georgia, Pirveli Balda (Samegrelo Region), 9 July 2017, 100 m^2, 375 m a.s.l., slope 65°, aspect 338°, 42.4892778° N, 42.4123611° E (± 10 m), soil pH 7.17, cover of rocks 65%, author: Dominik Zukal.

E_3 (85%): *Tilia begoniifolia* 4, *Castanea sativa* 2b, *Smilax excelsa* +, E_2 (5%): *Corylus avellana* 1, *Staphylea colchica* +, E_1 (65%): *Lamium galeobdolon* 3, *Asplenium scolopendrium* 2b, *Hedera helix* 2a, *Mercurialis perennis* 1, *Pteris cretica* 1, *Arabis nordmanniana* +, *Asplenium trichomanes* +, *Cardamine pectinata* s.l. +, *Carex digitata* +, *C. pendula* s.l. +, *Clinopodium umbrosum* +, *Oplismenus hirtellus* subsp. *undulatifolius* +, *Polypodium vulgare* s.l. +, *Polystichum aculeatum* +, *P. woronowii* +, *Ruscus colchicus* +, *Salvia glutinosa* +, *Smilax excelsa* +, *Staphylea colchica* juv. +, *Symphytum grandiflorum* +, *Dioscorea communis* r, *Hypericum androsaemum* r, *Moehringia trinervia* r; E_0 (45%).

***Polysticho aculeati-Tilietum begoniifoliae* ass. nov. hoc loco**

Polystichum aculeatum-Tilia begoniifolia community in this study

Holotypus: Relevé 14 in the Suppl. material 1. Georgia, Motsameta (Imereti Region), 24 July 2019, 100 m^2, 250 m a.s.l., slope 30°, aspect 90°, 42.2873611° N, 42.7590833° E (± 5 m), soil pH 7.66, cover of rocks 2%, author: Pavel Novák.

E_3 (85%), *Tilia begoniifolia* 4, *Carpinus betulus* 2a, *Acer cappadocicum* 2a, E_2 (1%) *Ilex colchica* +, *Smilax excelsa* +, *Ulmus minor* +, E_1 (50%) *Hedera colchica* 3, *Acer cappadocicum* juv. 1, *Ruscus colchicus* 1, *Asplenium scolopendrium* +, *Brachypodium sylvaticum* +, *Calystegia silvatica* +, *Carex flacca* +, *C. pendula* s.l. +, *Diospyros lotus* juv. +, *Polystichum aculeatum* +, *Pteris cretica* +, *Smilax excelsa* +, *Viola reichenbachiana* +, *Fraxinus excelsior* juv. r, E_0 (45%).

Conclusion

Based on phytosociological data, both original and extracted from literature, the study gives the first overview of the Colchic ravine forests (order *Aceretalia pseudoplatani*) in Georgia. We distinguished three communities of these azonal forests at the association level, predominantly reflecting geological and climatic settings. These communities constitute a new alliance *Pterido creticae-Tilion begoniifoliae*, which stands alongside several other endemic Colchic alliances of forest vegetation. They complement the so-far known vegetation diversity of the Colchic forests, one of the hotspots of Tertiary relict flora in the Northern Hemisphere. Our results could serve for biodiversity conservation, clarification of habitat definitions, management planning, and as a baseline for future habitat monitoring. Further attention should be paid to complex ecological research of Colchic forests, as a comprehensive understanding of their biodiversity is crucial for their effective conservation.

Data availability

The original field data for this study are located in the Suppl. material 1. The data are also available in the Transcaucasian Vegetation Database included in the GIVD and EVA (AS-00–005) core databases (https://euroveg.org/eva-database/databases).

Author contributions

PN conceived the idea of the study, performed the statistical analyses and led the writing, PN, VK and VT conducted the field sampling, DK and NM provided regional context of the study, while all authors critically revised the manuscript.

Acknowledgements

We are grateful to Kryštof Chytrý, Anna Hlaváčková, Jakub Salaš, Vojtěch Sedláček, and especially Dominik Zukal for their participating in the field sampling, to Jiří Danihelka, Libor Ekrt and Radomír Řepka for their help with the plant determination, and to Ketevan Batsatsashvili, Jana Ekhvaia and Otar Abdaladze for providing regional literature. Idoia Biurrun, Zdenka Preislerová, Martin Večeřa, Wolfgang Willner and three anonymous reviewers provided useful comments on previous versions of the study. The contribution of VT appears through the institutional support of long-term conceptual development of research institutions provided by the Ministry of Culture of the Czech Republic (ref. MK000094862)

References

Adamia S (Ed.) (2010) Geology of the Caucasus and adjacent area, 1: 250 000 scale geological map. In: Christofides G, Kantinaris N, Kostopoulos D, Chatzipetros A (Eds) Proceedings, XIX Congress of the Carpathian-Balkan Geological Association 99, Aristotle University of Thessaloniki, Thessaloniki, GR, 1–9.

Akhalkatsi M (2015) Forest habitat restoration in Georgia, Caucasus ecoregion. Mtsignobari, Tbilisi, GE, 102 pp.

Akhalkatsi M, Tarkhnishvili D (2012) Habitats of Georgia. GTZ, Tbilisi, GE, 118 pp.

Angiolini C, Foggi B, Viciani D (2012) *Acer-Fraxinus* dominated woods of the Italian peninsula: a floristic and phytogeographical analysis. Acta Societatis Botanicorum Poloniae 81: 123–130. https://doi.org/10.5586/asbp.2011.037

Anşin R (1979) Trabzon Meryem Ana Arastirma Ormani Florasi ve Saf Ladin Mescerelerinde Floristik Arastirmalar [Flora of Trabzon Meyremana Research Forest and Floristic Studies in Pure Spruce Stands]. Karadeniz Gazetecilik ve Matbaacılık, Trabzon, TR, 234 pp. [In Turkish]

Aznar-Sánchez JA, Belmonte-Ureña LJ, López-Serrano MJ, Velasco-Muñoz JF (2018) Forest ecosystem services: An analysis of worldwide research. Forests 9: e453. https://doi.org/10.3390/f9080453

Baran J, Pielech R, Bodziarczyk J (2018) No difference in plant species diversity between protected and managed ravine forests. Forest Ecology and Management 430: 587–593. https://doi.org/10.1016/j.foreco.2018.08.052

Bebiia SM (2022) Lesa Abkhazii [Forests of Abkhazia]. Akademia, Aḳəa, GE, 589 pp. [In Russian]

Biondi E, Casavecchia S, Pinzi M, Allegrezza M, Baldoni M (2002) The syntaxonomy of the mesophilous woods of the Central and Northern Apennines (Italy). Fitosociologia 39: 71–93.

Bokeria M (2010) West Georgia: History and diversity of vegetation and the use of plants through archaeobotany. In: Masserey C (Ed.) News of ancient Colchis. Archaeological, palaeobotanical and historical research, Georgian and Swiss cooperation. Adamantis, Tbilisi, GE, 21–31.

Bondyrev IV, Davitashvili ZV, Singh VP (2015) The geography of Georgia: problems and perspectives. Springer, Cham, CH, Heidelberg, DE, New York, US, Dordrecht, NL, London, UK, 228 pp. https://doi.org/10.1007/978-3-319-05413-1

Brun P, Zimmermann NE, Hari C, Pellisier L, Karger DN (2022a) CHELSA-BIOCLIM+ A novel set of global climate-related predictors at kilometre-resolution. EnviDat. https://envidat.ch/#/metadata/bioclim_plus [accessed 27 Sep 2023]

Brun P, Zimmermann NE, Hari C, Pellisier L, Karger DN (2022b) Global climate-related predictors at kilometre resolution for the past and future. Earth System Science Data 14: 5573–5603. https://doi.org/10.5194/essd-14-5573-2022

Campos JA, García-Mijangos I, Herrera M, Loidi J, Biurrun I (2011) Ravine forests (*Tilio-Acerion*) of the Iberian Peninsula. Plant Biosystems 145: 172–179. https://doi.org/10.1080/11263504.2011.602738

Chytrý M (Ed.) (2013) Vegetace České republiky 4. Lesní a křovinná vegetace [Vegetation of the Czech Republic 4. Forest and shrub vegetation]. Academia, Praha, CZ, 551 pp. [In Czech]

Chytrý M, Hájek M, Kočí M, Pešout P, Roleček J, Sádlo J, Šumberová K, Sychra J, Boublík K, … Chobot K (2019) Red list of habitats of the Czech Republic. Ecological Indicators 106: e105446. https://doi.org/10.1016/j.ecolind.2019.105446

Chytrý M, Tichý L, Hennekens SM, Knollová I, Janssen JAM, Rodwell JS, Peterka T, Marcenò C, Landucci F, … Schaminée JHJ (2020) EUNIS Habitat Classification: expert system, characteristic species combinations and distribution maps of European habitats. Applied Vegetation Science 23: 648–675. https://doi.org/10.1111/avsc.12519

Clot F (1990) Les érablaies européennes: essai de synthèse. Phytocoenologia 18: 409–564. https://doi.org/10.1127/phyto/18/1990/409

Çoban S, Willner W (2019) Numerical classification of the forest vegetation in the Western Euxine Region of Turkey. Phytocoenologia 49: 71–106. https://doi.org/10.1127/phyto/2018/0274

Coldea G (2015) Classe *Carpino-Fagetea*. In: Coldea G, Indreica A, Oprea A (Eds) Les associations végétales de Roumanie, Tome 3, Les associations forestiéres et arbustes. Presa Universitară Clujeană and Accent, Cluj-Napoca, RO, 70–125.

Connor SE, Thomas I, Kvavadze EV (2007) A 5600-yr history of changing vegetation, sea levels and human impacts from the Black Sea coast of Georgia. The Holocene 17: 25–36. https://doi.org/10.1177/0959683607073270

Council of Europe (2018) Revised Annex 1 to Resolution no. 4 (1996) listing endangered natural habitats requiring specific conservation measures. Standing Committee to The Council of Europe's Convention on the Conservation of European Wildlife and Natural Habitats, Strasbourg, FR.

Dengler J, Chytrý M, Ewald J (2008) Phytosociology. In: Jørgensen SE, Fath BD (Eds) Encyclopedia of ecology, 4. Elsevier, Oxford, UK, 2767–2779. https://doi.org/10.1016/B978-008045405-4.00533-4

Denk T, Frotzler N, Davitashvili N (2001) Vegetational patterns and distribution of relict taxa in humid temperate forests and wetlands of Georgia (Transcaucasia). Biological Journal of the Linnean Society 72: 287–332. https://doi.org/10.1006/bijl.2000.0502

Didukh YP (1996) Nemoralni lisy Girskogo Krymu klasu *Querco-Fagetea* Br.-Bl. et Vlieg. 1937 [Nemoral forests of the Mountainous Crimea of the class *Querco-Fagetea* Br.-Bl. et Vlieg. 1937]. Ukrayinskyi fitozenotychnyi zbirnyk Seriya A 3: 34–51. [In Ukrainian]

Didukh YP (Ed.) (2016) Biotopy Girskogo Krymu [Biotopes of the Crimean Mountains]. Nacionalna akademia nauk Ukrainy, Insitut botaniky imenia M. H. Kholodnoho, Kyiv, UA, 292 pp. [In Ukrainian]

Dolukhanov AG (1980) Kolkhidskii podlesok [Colchic understory]. Metsniereba, Tbilisi, GE, 261 pp. [In Russian]

Dolukhanov AG (2010) Lesnaya rastitelnost Gruzii [Forest vegetation of Georgia]. Universal, Tbilisi, GE, 532 pp. [In Russian]

EU4Environment (2024) Guidelines for managing forest habitats on Georgia's Emerald sites. International Bank for Reconstruction and Development/The World Bank, Washington DC, US, 66 pp.

Ermakov NB, Plugatar YV, Leiba VD, Ermakova EV (2021) Rastitelnye soobshchestva shirokolistvennykh lesov kolkhidskoi nizmennosti (zapadnoie zakavkazie) [Plant communities of broad-leaved forests of the Colchis Lowland (Western Transcaucasia)]. Biulleten GNBS 138: 39–49. https://doi.org/10.36305/0513-1634-2021-138-39-49 [In Russian]

Ermakov NB, Plugatar YV, Leiba VD (2023) Klassifikacia bukovykh (*Fagus orientalis*) lesov Zapadnogo Kavkaza [Classification of the beech (*Fagus orientalis*) forests of the Western Caucasus]. Rastitelnost Rossii 47: 112–132. https://doi.org/10.31111/vegrus/2023.47.112 [In Russian]

Fayvush G, Aleksanyan A (2016) Hayastani bnakmijavayrery [Habitats of Armenia]. National Academy of Sciences of the Republic of Armenia, Institute of Botany, Yerevan, AM, 358 pp. [In Russian]

Fischer HS (2015) On the combination of species cover values from different vegetation layers. Applied Vegetation Science 18: 169–170. https://doi.org/10.1111/avsc.12130

Gagnidze RI (2005) Vascular plants of Georgia. A nomenclatural checklist. Universali, Tbilisi, GE, 235 pp.

Gagnidze RI, Kemularia-Natadze LM (1985) Botanicheskaia geografiia i flora Racha-Lechkhumi [Phytogeography and flora of Racha-Lechkhumi]. Metsniereba, Tbilisi, GE, 147 pp. [In Russian]

Gegechkori A (2020) Biomes of the Caucasus: A comprehensive review. Nova Science Publisher, New York, US, 502 pp. https://doi.org/10.52305/LKTA3424

Ghafarian P, Azadi M, Meshkatee AH, Farahani MM (2012) Numerical simulation of the impact of Anatolian and Caucasus Mountains on the precipitation distribution over the Black Sea. Natural Hazards and Earth System Sciences 12: 607–613. https://doi.org/10.5194/nhess-12-607-2012

Gholizadeh H, Naqinezhad A, Chytrý M (2020) Classification of the Hyrcanian forest vegetation, Northern Iran. Applied Vegetation Science 23: 107–126. https://doi.org/10.1111/avsc.12469

Golitsyn SV (1935) Opyt botaniko-geograficheskogo kartirovania yugo-zapadnogo Kavkaza [Attemp of botanical and geographic mapping of the southwestern Caucasus]. Trudy Voronezhskogo Gosudarstvennogo Universiteta 6: 166 –237. [In Russian]

Gorgiladze L, Meparishvili G, Sikharulidze Z, Natsarishvili K, Davitadze R (2011) First report of box blight caused by *Cylindrocladium buxicola* in Georgia. New Disease Reports 23: 24. https://doi.org/10.5197/j.2044-0588.2011.023.024

Gulisashvili VZ, Makhatadze LB, Prilipko LI (1975) Rastitelnost Kavkaza [Vegetation of the Caucasus]. Nauka, Moskva, RU, 232 pp. [In Russian]

Güngöroğlu (Ed.) (2018) Practicability of the EU Natura 2000 concept in the forested areas of Turkey. Türkiye Ormancılar Derneği, Ankara, TR, 292 pp.

Hennekens SM, Schaminée JHJ (2001) TURBOVEG, a comprehensive database management system for vegetation data. Journal of Vegetation Science 12: 589–591. https://doi.org/10.2307/3237010

Hill MO, Bunce RGH, Shaw MW (1975) Indicator species analysis, a divisive polythetic method of classification, and its application to a survey of native pinewoods in Scotland. Journal of Ecology 63: 597–613. https://doi.org/10.2307/2258738

Janssen JAM, Rodwell JS, Criado MG, Gubbay S, Haynes T, Nieto A, Sanders N, Landucci F, Loidi J, … Valachovič M (2016) European Red List of Habitats: Part 2. Terrestrial and freshwater habitats. Publications Office of the European Union, Luxembourg. LU, 38 pp. http://dx.doi.org/10.2779/091372

Karami-Kordalivand P, Esmailzadeh O, Willner W, Noroozi J, Alavi SJ (2021) Classification of forest communities (co-)dominated by *Taxus baccata* in the Hyrcanian forests (northern Iran) and their comparison with southern Europe. European Journal of Forest Research 140: 463–476. https://doi.org/10.1007/s10342-020-01343-y

Kavgacı A, Karaköse M, Seda Keleş E, Balpınar N, Arslan M, Yalçın E, Novák P, Čarni A (2023) Classification of forest and shrubland vegetation in central and eastern Euxine Turkey and SW Georgia. Applied Vegetation Science 26: e12753. https://doi.org/10.1111/avsc.12753

Kikodze D, Memiadze N, Kharazishvili D, Manvelidze Z, Müller-Schärer H (2010) The alien flora of Georgia. 2nd edn. Joint SNSF SCOPES and FOEN publication, Ascona, CH, Tbilisi GE, 36 pp.

Kikvidze Z, Ohshawa M (2001) Richness of Colchic vegetation: comparison between refugia of south-western and East Asia. BMC Ecology 1: 1–10. https://doi.org/10.1186/1472-6785-1-6

Kolakovskii AA (1961) Rastitelnyi mir Kolkhidy [The flora and vegetation of Colchida]. Izdatelstvo Moskovskogo Universiteta, Moskva, RU, 459 pp. [In Russian]

Korkmaz H, Yalçin E, Kutbay HG, Berk E, Bilgin A (2008) Contribution to the knowledge of the syntaxonomy and ecology of macchie and forest vegetation in Paphlagonia, North Anatolia, Turkey. Acta Botanica Gallica 155: 495–512. https://doi.org/10.1080/12538078.2008.10516129

Košir P, Čarni A, Di Pietro R (2008) Classification and phytogeographical differentiation of broad-leaved ravine forests in southeastern Europe. Journal of Vegetation Science 19: 331–342. https://doi.org/10.3170/2008-8-18372

Lance GN, Williams WT (1967) A general theory of classificatory sorting strategies. I. Hierarchical systems. Computer Journal 9: 373–380. https://doi.org/10.1093/comjnl/9.4.373

Leuschner C, Ellenberg H (2017) Ecology of Central European forests. Springer, Berlin and Heidelberg, DE, 972 pp. https://doi.org/10.1007/978-3-319-43042-3

Maleev PV (1938) Rastitelnost prichernomorskikh stran (Evksinskoi provincii Sredizemnomoria), ee proiskhozhdenie i sviazi [Vegetation of the Black Sea countries (Euxinian province of the Mediterranean), its origins and connections]. Trudy botanicheskogo instituta AN SSSR ser. 3, vol. 4: 136–252. [In Russian]

Matsiakh I, Kramarets V, Mamadashvili G (2018) Box tree moth *Cydalima perspectalis* as a threat to the native populations of *Buxus colchica* in Republic of Georgia. Journal of the Entomological Research Society 20: 29–42.

MEPA (Ministry of Environmental Protection and Agriculture of Georgia) (2023) First national forest inventory in Georgia. 2023. MEPA, Tbilisi, GE, 122 pp.

Millar SWS (2014) Colluvial deposit. Hargitai H, Kereszturi Á (Eds) Encyclopedia of planetary landforms. Springer, New York, US, 1–10. https://doi.org/10.1007/978-1-4614-9213-9_55-1

Milne RI (2006) Northern hemisphere plant disjunctions: a window on tertiary land bridges and climate change? Annals of Botany 98: 465–472. https://doi.org/10.1093/aob/mcl148

Milne RI, Abbott RJ (2002) The origin and evolution of tertiary relict floras. Advances in Botanical Research 38: 281–314. https://doi.org/10.1016/S0065-2296(02)38033-9

Mittermeier RA, Robles Gil P, Hoffmann M, Pilgrim J, Brooks T, Mittermeier CG, Lamoreux J, da Fonseca GAB (2004) Hotspots revisited: Earth's biologically richest and most endangered ecoregions. CEMEX, Mexico City, MX, 392 pp.

Mucina L, Bültmann H, Dierßen K, Theurillat J-P, Raus T, Čarni A, Šumberová K, Willner W, Dengler J, … Tichý L (2016) Vegetation of Europe: Hierarchical floristic classification system of vascular plant, bryophyte, lichen, and algal communities. Applied Vegetation Science 19 (suppl. 1): 3–264. https://doi.org/10.1111/avsc.12257

Mumladze D, Lomidze N (2012) Klimatis tipebis ruka [Climate types map]. In: Gobejishvili R (Ed.) Sakartvelos erovnuli at'lasi [The National Atlas of Georgia]. Kartographia, Tbilisi, GE, 47. [In Georgian]

Nakhutsrishvili G (2013) The vegetation of Georgia (South Caucasus). Springer, Berlin, DE, 235 pp. https://doi.org/10.1007/978-3-642-29915-5

Nakhutsrishvili G, Zazaznashvili N, Batsatsashvili K (2011) Regional profile: Colchic and Hyrcanian temperate rainforest of the Western

Eurasian Caucasus. In: DellaSala DA (Ed.) Temperate and boreal rainforests of the world: ecology and conservation. Island Press, Washington DC, US, 212–221.

Nakhutsrishvili G, Zazanashvili N, Batsatsashvili K, Montalvo CS (2015) Colchic and Hyrcanian forests of the Caucasus: similarities, differences and conservation status. Flora Mediterranea 25: 185–192. https://doi.org/10.7320/FlMedit25SI.185

Nakhutsrishvili G, Abdaladze O, Batsatsashvili K, Dzadzamia L (Eds) (2024) Natural forests of Georgia (the South Caucasus). Ilia State University Press, Tbilisi, GE, 224 pp.

Neuhäuslová-Novotná Z (1974) Beitrag zur Kenntnis des *Arunco silvestris-Alnetum glutinosae* in der Tschechischen Sozialistischen Republik (ČSR). Folia Geobotanica et Phytotaxonomica 9: 217–230. https://doi.org/10.1007/BF02853144

Novák P, Zukal D, Kalníková V, Chytrý K, Kavgacı A (2019) Ecology and syntaxonomy of Colchic forests in south-western Georgia (Caucasus region). Phytocoenologia 49: 231–248. https://doi.org/10.1127/phyto/2019/0250

Novák P, Zukal D, Harásek M, Vlčková P, Abdaladze O, Willner W (2020) Ecology and vegetation types of oak-hornbeam and ravine forests of the Eastern Greater Caucasus, Georgia. Folia Geobotanica 55: 333–349. https://doi.org/10.1007/s12224-020-09386-0

Novák P, Stupar V, Kalníková V (2021a) *Carpinus orientalis* forests in Georgian Colchis: First insights. Tuexenia 41: 37–51. https://doi.org/10.14471/2021.41.012

Novák P, Zukal D, Harásek M, Vlčková P, Abdaladze O, Willner W (2021b) Correction to: "Ecology and vegetation types of oak-hornbeam and ravine forests of the Eastern Greater Caucasus, Georgia". Folia Geobotanica 56: 97. https://doi.org/10.1007/s12224-021-09391-x

Novák P, Kalníková V, Szokala D, Aleksanyan A, Batsatsashvili K, Fayvush G, Kolbaia S, Nakhutsrishvili G, Sedláček V, … Zukal D (2023a) Transcaucasian Vegetation Database – a phytosociological database of the Southern Caucasus. Vegetation Classification and Survey 4: 231–240. https://doi.org/10.3897/VCS.105521

Novák P, Kalníková V, Večeřa M, Štětková G, Sedláček V, Pustková Š, Szokala D, Peška P, Štěrba T, … Gogoladze A (2023b) Alluvial alder forests of the Greater Caucasus, Georgia: ecology, habitats and variability. Tuexenia 43: 9–32. https://doi.org/10.14471/2023.43.003

Novák P, Willner W, Biurrun I, Gholizadeh H, Heinken T, Jandt U, Kollár J, Kozhevnikova M, Naqinezhad A, … Chytrý M (2023c) Classification of European oak–hornbeam forests and related vegetation types. Applied Vegetation Science 26: e12712. https://doi.org/10.1111/avsc.12712

Novák P, Večeřa M, Gholizadeh H, Pustková Š, Szokala D, Kharazishvili D, Memiadze N, Sedláček V, Kalníková V (2024) Forests of the Tertiary relict tree *Zelkova carpinifolia* in Colchis (South Caucasus) and their regional vegetation context. Tuexenia 44: 9–32. https://doi.org/10.14471/2024.44.007

Ogle DH, Wheeler P, Dinno A (2023) FSA: simple fisheries stock assessment methods. R package version 0.9.5. https://cran.r-project.org/web/packages/FSA/index.html [accessed 28 Nov 2024]

Oksanen J, Simson GL, Guillaume Blanchet F, Kindt R, Legendre P, Minchin PR, O'Hara RB, Solymos P, Stevens MHH, … Weedon J (2022) vegan: Community Ecology Package. R package version 2.6-4. cran.r-project.org/web/packages/vegan/ [accessed 11 Nov 2023]

Parliament of Georgia (2020) Forest Code of Georgia. No. 5949-SS of 2020. Government of Georgia, Tbilisi, GE, 41 pp.

QGIS Development Team (2018) QGIS geographic information system. Open source geospatial foundation project. http://qgis.osgeo.org [accessed 12 Nov 2020]

Quézel P, Barbero M, Akman Y (1980) Contribution a l'etude de la vegetation forestiere d'Anatolie Septentrionale. Phytocoenologia 8: 365–519. https://doi.org/10.1127/phyto/8/1980/365

Quézel P, Barbero M, Akman Y (1992) Typification de syntaxa décrits en région méditerranéenne orientale. Ecologia Mediterranea 18: 81–87. https://doi.org/10.3406/ecmed.1992.1708

R Core Team (2022) R: A language and environment for statistical computing. Ver. 4.0.2. R Foundation for Statistical Computing. http://www.R-project.org [accessed 12 Dec 2022]

Roleček J, Tichý L, Zelený D, Chytrý M (2009) Modified TWINSPAN classification in which the hierarchy respects cluster heterogeneity. Journal of Vegetation Science 20: 596–602. https://doi.org/10.1111/j.1654-1103.2009.01062.x

Rübel EA (1914) The forests of the Western Caucasus. Journal of Ecology 2: 39–42. https://doi.org/10.2307/2255372

Sinskaia EN (1933) Osnovnye cherty evolucii lesnoi rastitelnosti Kavkaza v sviazi I istoriei vidov II [The main features of the evolution of forest vegetation]. Botanicheskii Zhurnal SSSR 18/6: 487–515. [In Russian]

Sokal RR, Rohlf FJ (1995) Biometry: The principles and practice of statistics in biological research. 3rd edn. W.H. Freeman and Co., New York, US, 887 pp.

Sokhadze EV, Sokhadze ME (1964) K botaniko-geograficheskoi kharakteristike gornoi chasti izvestniakov zapadnoi Gruzii [On the botanico-geographic characteristic of mountain part of the limestone areas in western Georgia]. Trudy instituta geografii imenia Vakhushti Bagrationi Tbilisi 20: 105–118. [In Russian]

Stefańska-Krzaczek E, Kącki Z, Szypuła B (2016) Coexistence of ancient forest species as an indicator of high species richness. Forest Ecology and Management 365: 12–21. https://doi.org/10.1016/j.foreco.2016.01.012

Takhtajan A (1986) Floristic regions of the world. University of California Press, Berkeley, US, 522 pp.

Tarasov PE, Volkova VS, Webb T, Guiot J, Andreev AA, Bezusko LG, Bezusko TV, Bykova GV, Dorofeyuk NI, … Sevastyanov DV (2000) Last glacial maximum biomes reconstructed from pollen and plant macrofossil data from northern Eurasia. Journal of Biogeography 27: 609–620. https://doi.org/10.1046/j.1365-2699.2000.00429.x

Thalmann DJK, Kikodze D, Khutsishvili M, Kharazishvili D, Guisan A, Broennimann O, Müller-Schärer H (2015) Areas of high conservation value in Georgia: present and future threats by invasive alien plants. Biological Invasions 17: 1041–1054. https://doi.org/10.1007/s10530-014-0774-2

Theurillat JP, Willner W, Fernández-González F, Bültmann H, Čarni A, Gigante D, Mucina L, Weber H (2021) International Code of Phytosociological Nomenclature. 4th edn. Applied Vegetation Science 24: e12491. https://doi.org/10.1111/avsc.12491

Tichý L (2002) JUICE, software for vegetation classification. Journal of Vegetation Science 13: 451–453. https://doi.org/10.1111/j.1654-1103.2002.tb02069.x

Tichý L, Chytrý M (2006) Statistical determination of diagnostic species for site groups of unequal size. Journal of Vegetation Science 17: 809–818. https://doi.org/10.1111/j.1654-1103.2006.tb02504.x

Tichý L, Chytrý M, Hájek M, Talbot SS, Botta-Dukát Z (2010) OptimClass: using species-to-cluster fidelity to determine the optimal partition in classification of ecological communities. Journal of Vegetation Science 21: 287–299. https://doi.org/10.1111/j.1654-103.2009.01143.x

Tichý L, Jason H, Nejezchlebová M (2011) Juice. Program for management, analysis and classification of ecological data. Second edition of the Program Manual. First part. Department of Botany and Zoology, Brno, CZ. https://www.sci.muni.cz/botany/juice/JCman2011_1st.pdf [accessed 21 Aug 2024]

Tichý L, Hennekens SM, Novák P, Rodwell JS, Schaminée JHJ, Chytrý M (2020) Optimal transformation of species cover for vegetation classification. Applied Vegetation Science 23: 710–717. https://doi.org/10.1111/avsc.12510

Tielidze L (Ed.) (2019) Geomorphology of Georgia. Springer, Cham, CH, 289 pp. https://doi.org/10.1007/978-3-319-77764-1

Tüxen R (1957) Der Geissbart-Schwarzerlenwald (*Arunco-Alnetum glutinosae* [Kästner 1938]). Mitteilungen der Floristisch-soziologischen Arbeitsgemeinschaft 6/7: 258–263.

Valachovič M, Kliment J, Hegedüšová Vantarová K (2021) Rastlinné spoločenstvá Slovenska. 6. Vegetácia lesov a krovín [Plant communitites of Slovakia. 6. Forest and shrub vegetation]. Veda, Bratislava, SK, 766 pp. [In Slovak]

Večeřa M, Divíšek J, Lenoir J, Jiménez-Alfaro B, Biurrun I, Knollová I, Agrillo E, Campos JA, Čarni A, … Chytrý M (2019) Alpha diversity of vascular plants in European forests. Journal of Biogeography 46: 1919–1935. https://doi.org/10.1111/jbi.13624

Vetters H, Tribsch A (2008) *Staphylea pinnata* and *S. colchica*, the two European bladdernuts: Insights in chorology, population genetic aspects and growth forms. Sauteria 16: 407–409.

Ward JH Jr (1963) Hierarchical grouping to optimize an objective function. Journal of American Statistical Association 58: 236–244. https://doi.org/10.1080/01621459.1963.10500845

Willner W (2020) What is an alliance? Vegetation Classification and Survey 1: 139–144. https://doi.org/10.3897/VCS/2020/56372

Willner W, Grabherr G (Eds) (2007) Die Wälder und Gebüsche Österreichs. Ein Bestimmungswerk mit Tabellen. Spektrum Akademischer Verlag, Heidelberg, DE, 608 pp.

Willner W, Jiménez-Alfaro B, Agrillo E, Biurrun I, Campos JA, Čarni A, Casella L, Csiky J, Ćušterevska R, … Chytrý M (2017) Classification of European beech forests: a Gordian Knot? Applied Vegetation Science 20: 494–512. https://doi.org/10.1111/avsc.12299

Zazanashvili N (1999) On the Colkhic vegetation. In: Klötzli F, Walther G-R (Eds) Conference on recent shifts in vegetation boundaries of deciduous forests, especially due to general global warming. Birkhäuser, Basel, CH, 181–197. https://doi.org/10.1007/978-3-0348-8722-9_11

Zukal D, Novák P, Duchoň M, Blanár D, Chytrý M (2020) Calcicolous rock-outcrop lime forests of east-central Europe. Preslia 92: 191–211. https://doi.org/10.23855/preslia.2020.191

E-mail and ORCID

Pavel Novák (Corresponding author, pavenow@seznam.cz), ORCID: https://orcid.org/0000-0002-3758-5757
Veronika Kalníková (V.Kalnikova@seznam.cz), ORCID: https://orcid.org/0000-0003-2361-0816
Vojtěch Taraška (vojtech.taraska@centrum.cz), ORCID: https://orcid.org/0000-0001-5744-3943
Nino Memiadze (ninovaja@gmail.com), ORCID: https://orcid.org/0009-0004-6330-9598
Davit Kharazishvili (davit.kharazishvili@gmail.com), ORCID: https://orcid.org/0000-0001-9254-9954

Supplementary material

Supplementary material 1
Original field data (*.xlsx)
Link: https://doi.org/10.3897/VCS.154417.suppl1

Supplementary material 2
Details on the plots extracted from the literature (*.doc)
Link: https://doi.org/10.3897/VCS.154417.suppl2

Supplementary material 3
Aggregated taxa (*.doc)
Link: https://doi.org/10.3897/VCS.154417.suppl3

Supplementary material 4
Lists of diagnostic, constant and dominant species of the Colchic ravine forest communities (*.doc)
Link: https://doi.org/10.3897/VCS.154417.suppl4

Supplementary material 5
Full synoptic table of the Colchic ravine forest communities (*.xlsx)
Link: https://doi.org/10.3897/VCS.154417.suppl5

Supplementary material 6
Synoptic table of the alliances recognized in the Regional Forests dataset (*.xlsx)
Link: https://doi.org/10.3897/VCS.154417.suppl6